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BULLETIN
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TORREY BOTANICAL CLUB

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The Concept of the Genus [1]

I. History of the Generic Concept in Botany [2]

HARLEY HARRIS BARTLETT

The concept of the genus must be as old as folk science itself. Certainly we find a nomenclature for plants and animals that is hardly different from modern scientific nomenclature among many peoples and in many languages.

It would be quite futile to speculate at too great length about how generic grouping had its beginnings, but there are two processes that must have been operative in ancient times just as they are today. (1) With enlarging experience, people make finer distinctions, and need different names for newly distinguished entities which have previously been called by the same original name. The original name becomes generic in its application; variously qualified it provides the basis for specific names. Thus genera are set up by analysis. (2) As language becomes cumbersomely rich in separate names for closely similar things, there is a tendency toward grouping or classification under the same name on the basis of newly perceived similarities. Thus genera are set up by synthesis. Many kinds of grass are so similar that we can hardly believe that the concept "grass" was not more ancient than the distinction of particular kinds. Here we have a hypothetical instance of the origin of a folk-science genus by analysis. On the contrary, the generic concept "fern" is a technical one, depending upon close observation, so when we find a people of relatively low culture, such as the Batak of Sumatra, defining extremely diverse plants as

[1] Papers presented at a Symposium of the Botanical Society of America, Systematic Section, and the American Society of Plant Taxonomists at Indianapolis, December 29, 1937.

[2] Papers from the Department of Botany of the University of Michigan, no. 713.

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"fern" pretty much as the modern botanist does, on the basis of a relatively obscure characteristic, namely, the leaf-borne sporangia, we feel sure that a genus has been set up by synthesis of things superficially very unlike.

The grouping of distinguishable but similar kinds into genera seems always to have been a linguistic necessity if there was to be reasonable flexibility and precision in the nomenclature of plants and animals. The flexible and undefined categories genus and species ever sufficed for most purposes of folk science, and so we find by the analysis of common speech that only these two are indicated in the plant nomenclature of most languages.

The scientific concept of the genus is therefore not modern at all. It did not originate with Linnaeus or with his great predecessor, Tournefort. Rather, the nomenclatural reforms of both brought the Latin names of plants back into conformity with the usages of common speech, a conformity which had existed in science at the beginning of the sixteenth century but was gradually lost through the two centuries that intervened between the German Fathers of Botany and the great reformer, Linnaeus.

Complete scientific systematization of plants and animals has brought into recognition higher or more inclusive categories than the genus. Folk science had a vague need for these, and sometimes recognized their existence, as in instances that will later be briefly alluded to. Nevertheless, in speaking of the generic concept in folk botany as needing little change to become essentially the generic concept of modern science, I must of course guard myself by insisting that the inclusiveness or size of genera, now as in the past, is less a matter of science than of linguistic preference and convenience.

Classical botany was folk science. It did not progress far beyond the gathering together of folk beliefs and practical information. Theophrastus dealt almost entirely with cultivated plants, and Dioscorides with medicinal ones, and each systematized the knowledge or belief of his time with regard to the particular plants that interested him. Although they had no Dioscorides to record it, the illiterate barbarians of northern Europe probably had a folk science and terminology nearly as extensive and useful as that of Greece or Italy. Contemporaneously, an equivalent folk science would have been found in Egypt, in Ethiopia, in Palestine, in Persia, in Mesopotamia. There is, as a matter of fact, a modern interpretation of an old Babylonian herbal. China has its ancient knowledge of plants with a surviving literary record in a long series of printed Pênts'ao or herbals dating back at least to 1100, and based upon folk science hundreds or thousands of years older. China passed its learning on to Japan, where there was certainly already a native lore which was grafted upon the Chinese. India

early had systems of native medicine and associated plant lore which have come down to the present time partly by way of literature and partly by way of tradition. Anyone who delves into the beliefs of the peoples of the East Indies cannot fail to be impressed by the voluminous lore of plants, comparable in extent and value to that of the classical Greeks or Romans, and maintained by a nomenclature quite as scientific as the best in European botany during the time preceding Linnaeus. The New World had developed its own plant lore, an extensive body indeed in ancient Mexico, with its associated system of plant names and plant classification. Wherever we look into the matter, whatever the people or the language, we find naming and classification of plants, and almost invariably a more or less well-defined idea of the genus, as the smallest group that almost everyone might be expected to have the name for in his vocabulary. It might or might not be subdivided into species.

The idea that the generic concept is a characteristic of folk science will be found carefully developed in E. L. Greene's *Landmarks of Botanical History*. I have carried the development somewhat farther, anxious to show that the generic idea is concerned in its beginnings with the psychology of language, that those beginnings are lost in pre-history, and that we can only recover some conception of them by the consideration and comparative study of the plant names of people everywhere.

The tendency to group plants into named genera, so generally characteristic of human thought and language, reflects the fact that there are not enough different words in the living, current vocabulary of any language to supply each closely similar plant with a basically distinctive name. We, for example, apply the name oak to many different trees, but so long as we stay in our own proper north-temperate habitat, our generic feeling for the oaks is true and consistent. As a matter of fact, Greene has shown that the generic idea "oak," as held today, was really borrowed by scientific systematic botany from the folk science of the English pioneer settlers in temperate America, who extended the English folk concept of "oak" to cover the various widely different American oaks. In the eastern United States we distinguish white oak, burr oak, chestnut oak, live oak, scarlet oak, black oak, shingle oak and others, having a perfect binomial nomenclature for them in English, and, from the literary record, we may be sure that these designations owe nothing to scientific botany. They were in use in folk science before the botanists with their imperfect materials had anywhere nearly as good an idea of the oak species as the English colonists in the American woods.

In this instance the generic concept came from England, where there were only a couple of closely allied oaks, and was successfully applied to a multitude of popularly distinguished species. The botanists had long

labored under the difficulty of trying to recognize as many genera as there were Latin words for the few but exceedingly distinct oaks of Europe, namely, suber, ilex, cerris, robur, and quercus. We have here one example from folk science of the linguistic advantage of a large genus over several small genera. The generic concept is a variable thing in popular consciousness, as in science, but probably more uniformly and consistently applied in the folk science of most countries than in the systematic botany of the sixteenth and seventeenth centuries. We need have no doubt that ancient Latin and Greek folk botany, only imperfectly preserved in the literary record, were much more complete and perfect than the medieval "scientific" botany which in countries remote from the Mediterranean basin forced vaguely understood Greek and Latin nomenclature upon the plants of Germany and other parts of northern Europe. Likewise we may be sure that the folk science of unsophisticated peasants in almost any place in Europe, in any period of the Middle Ages, if it had ever been painstakingly and completely recorded, would have been better, from the standpoint of system, recognition of natural genera, and nomenclature, than the degenerated classical botany of the sophisticated at the same time.

Beginning with the great German botanists of the sixteenth century, the more the botanists broke away from the shackles of the completely decadent literary tradition, the more ready they were to make a beginning in good systematic botany by translating into Latin the names of plants that the common man knew, and knew not merely as species but also in groups, for which there were vernacular generic names. Reverting to the example drawn from our oaks, the folk botany of the American pioneer gave botany eventually not only such species concepts as those of *Quercus coccinea*, scarlet oak, *Quercus imbricaria*, shingle oak, and *Quercus tinctoria*, dyer's oak, but the generic concept implied by the adoption of these translated names. Many unnatural concepts of the late medieval botanists in time came to be corrected by adoption of popular concepts that were better than the quasi-scientific. To jump over several centuries in our argument, for the sake of driving the point home, it may be pointed out that Linnaeus, who followed folk botany in the matter of the oaks, followed pseudo-classical medieval tradition in disregarding it when he made the classical name Juglans do service for both the walnuts and the newly discovered hickories of the New World. It was not long after the time of Linnaeus that the popular generic conceptions of "hickory" and "walnut" superseded his earlier and unnatural forcing of the hickories into *Juglans*. The popular generic concepts of "sumac" and "poison-ivy" are now by way of prevailing over the impossibly inclusive *Rhus* that many scientists have held even down to the present. Although it would be absurd to force

the idea too far, it is clear that folk nomenclature may provide good indications not only for practical but for scientific generic grouping.

In whatever race or country we look for it, we find the classificatory instinct more or less strongly developed, and finding expression in the grouping of species into genera. There is everywhere a tendency to group similar species under generic names, and to name the species by using some linguistic device not unlike the binomial nomenclature of Linnaeus. There would seem to be a good psychological basis for binomial nomenclature. As many basically distinct words will be current in each vernacular as an intelligent speaker (or better, perhaps, the total of those persons of diversified experience and occupation who speak a vernacular) can attach ideas to. These basic plant names are not enough to go around. Therefore grouping into genera is linguistically and psychologically inevitable, whether the grouping results from failure to see differences or from especially keen apprehension of similarities.

Recently I have been giving much attention to the climbing palms of the Malayan region. Since these plants are very different from each other in their utilities, it is natural that they should be critically systematized by the native peoples who live where they grow. Ordinarily they form, popularly, only a single genus, which may be called *rotang* (we get our English word "rattan" from this), or *hotang*, or *uwai*. Under the genus are arrayed the species, *hotang soga*, *hotang djorlang*, *hotang sumambu*, *hotang ahonir*, *hotang taritting*, *hotang pahoe* and many others, to cite only part of the names from a single place and dialect.[1] The distinctions are known to most of the people of the forest, and are based upon many of the same morphological features that would be utilized in classification by a trained botanist. Of all the plants called *hotang* (in the district of the east coast of Sumatra where I am best acquainted with people and flora) only one, *hotang da ursa*, is not a climbing palm, but it is *Flagellaria*, a climbing, monocotyledonous plant recognized by the natives as so different that *hotang da ursa* is itself treated as a genus. Whereas any of the climbing palms may be called simply hotang, the *Flagellaria* may not be. It must be called by its full name, *hotang da ursa*. Here we get an inking of how generic designations of more than one word arose in other languages.

In these names of the climbing palms we have a paradigm to illustrate the working of the human mind in arriving at a classification and nomenclature of plants. We see the interplay and balance between the limitations of vocabulary, on the one hand, and comprehension of differences among a multiplicity of interesting and useful natural objects, on the other. The number of basically independent words that can be sufficiently utilized to

[1] Pardembanan dialect (a sub-Toba dialect) of Asahan, Sumatra.

be retained in the vocabulary is so much more limited than the objects for which names are needed that a binomial system develops as a matter of course. Among the Batak the grouping of inconsequential things is very inclusive. For instance, "*duhut*" will do for a wide range of weeds or herbaceous plants, but scores or hundreds of kinds of *duhut* that are important enough so that they must be talked about have generic and specific names. *Pahu* will do as the generic name for almost any fern, but a great many species and a few restricted genera are recognized. Even such an aberrant thing as *Ceratopteris* is recognized as a fern. *Saio* is *Selaginella*. It is recognized that there are several closely similar kinds, but nobody bothers to give them names. (Until recently the botanists did not, either!) An inclusive generic name for almost all moss-like plants is *lumut*. Classification of *lumut* is hardly attempted, but the conspicuous *Leucobryum* has a generic name. The condition of moss nomenclature is after all not so very different from that in scientific systematic botany before Dillenius. As to plants in general, there is a partial classification, going to genera or species in hundreds of instances, but leaving many plants unclassified, regarding which all that the native botanist will say is that they are trees, herbs, vines, ferns, or mosses. Any very slender sedge is *si martihe-tihe*, "the one who passes for *tihe*" or "the tihe-like one" (*tihe* being a particular kind of sedge) and many other designations of this sort are very broadly but discriminatingly classificatory. Here we have an inkling of the family concept and a name which is linguistically a reflection of the same kind of thinking that gave us the botanical family names in current scientific use. But we are concerned with genera, and must not digress too far.

To repeat, the generic concept is so useful in classifying knowledge and has been so logically and extensively applied in various parts of the world, that to trace its history would be to trace the history of language and thought itself. All that we can profitably do by way of tracing the concept as it is reflected in scientific botanical nomenclature is to review the status of genera in works of some of the great botanists who preceded Linnaeus, to show that Linnaeus based his clear concepts of genera largely upon Tournefort and Plumier, and that his reform in nomenclature was a reversion to ancient simplicity of speech, and to point out that in the main the changes that have come about since Linnaeus have been to define genera as groups of species that do not seem to violate the conceptions of natural affinity by descent that were developed by Darwin.

Let us begin with the work of the first of the German Fathers, Brunfels, whose great herbal was first published in 1532. In discussing his work, I wish to make an important point clear at the outset, namely, that his generic names were generally but not always single words. During the

middle ages the language in common use for learned books was Latin. Latin has only a small store of original plant names and does not readily lend itself to the formation of new ones, as Greek does. In Latin, therefore, many genera had two-word names, and to name a species, by adding a qualifying term to the generic name, required the use of at least three words. Brunfels replaced some, but not all, of the confusing two-word Latin generic names by single words. He left, for instance, the two-word generic names *Sigillum Salomonis*, "Solomon's seal," and *Bursa Pastoris*, "shepherd's purse."

Even if Brunfels' genera are not always such, according to our modern evolutionary ideas of plant affinities, they often conform exactly to modern genera, or at least their species belong to the same family. Thus he had a mallow, which, being in his opinion the true *Malva* of the ancients, he called simply *Malva*, with no qualifying designation, whereas a second species he called *Malva equina*, "horse mallow." In the Latin edition of his herbal he gives a German nomenclature that corresponds exactly to the Latin names, namely, *Bappelen* and *Rossbappelen*. If, however, we turn to the German edition, the nomenclature is more in accord with Linnaean and modern usage. The true *Malva* is *Gaenssbappelen*, "goose-mallow," and the other is *Rossbappelen*, "horse-mallow." We have specific names made in a Teutonic way by compounding an adjective modifier with the generic name rather than in the Latin manner, which keeps the words separate, but the basic idea of qualifying a generic name to make a specific one is there. Brunfels has examples of both ways, in his German edition. We do not find complete consistency in Brunfels' work, but enough to show that he had the modern idea of the genus, as a group with morphological similarities, within which the species were grouped. Furthermore, he arrived at the more modern features of his work by turning German common names, of the sort just cited, into Latin. The result of necessity resembled the Linnaean binomial system if the generic name was only a single word, for then the addition of one qualifying term made a binomial specific name of quite modern aspect.

We find *Helleborus niger*, for example, and *Plantago major*, names which meant to Brunfels in the year 1532 just what they mean to us now. One of the most interesting points in connection with Brunfels' nomenclature is that it displays the generic concept quite as definitely in German as in Latin. A glance through the German edition brings to light such genera as *Seeblüm* for the water lilies, the species being two, the white and the yellow. They are separate genera in the eyes of modern botanists, but in German folk botany, as reflected by common names, they constituted a genus of two species. We find two primroses, *Geel Hymmelschlüssel* and *Weiss Hymmelschlüssel*, a perfectly good example of the generic concept

as well as of binomial nomenclature, and, a few pages farther on, *Edler Augentrost* and *Weisszer Augentrost*. Here, according to modern ideas, the genera are different but the family is the same. The important point is that it is quite as characteristic of folk botany as of modern systematic science to classify to the genus, which is more or less consciously thought of as the smallest grouping requiring a distinctive name. Within the genus, if the distinction of several kinds is necessary, a qualifying designation is used and the whole name becomes a binomial. If there is but one sort within a genus, no qualifying word is necessary, for the generic name is sufficient. Brunfels did not try to invent Latin names for plant genera that perhaps the ancients did not know. He was satisfied to call the little *Draba verna* of later botanists merely *Gaenssblum*, and Adanson, the radical in botanical nomenclature, who did not care whether nomenclature was Latin or not, took this German name as the valid scientific one for the genus, attributing it to Brunfels. For another plant that Brunfels found no name for, not even in German, he was content to say that the name was unknown. That was equivalent to recognizing its generic distinctness from the other plants in his herbal, even though he does not go to the length of naming it. It was the first published record of *Anemone nemorosa*. There is little evidence that Brunfels' botanical knowledge, aside from his efforts to identify most of his plants with those known to classical writers, was other than a very intelligent sifting of current folk botany. His definite attempts at classifying similar plants into genera we may think of as expressing the natural tendency of Germanic thought and language. His recording of what appears to be genuine folk science represented an immense improvement over the debased travesty of classical botany which, constantly vitiated by gross error, superstition and fraud, had reached an unbelievably low level in some of the works of the type of the *Hortus Sanitatis*.

This glimpse at Brunfels' simple and practical generic ideas and terminology must suffice for his century. Unfortunately many of his successors continued in vain the process of trying to squeeze plants totally unknown into old genera, with the result that the simplicity and clarity of Brunfels' work soon disappeared. Scientific botany became more and more involved. The generic idea, so clear in most folk botany, became less so, and specific names, long and rambling ones, did not necessarily incorporate the generic name at all.

In 1623 the learned Caspar Bauhin published his *Pinax Theatri Botanici*, a work on which he spent forty laborious years. It was an index to all plants known up to his time, listing all the supposed synonymy. As the title indicates, it was but a prepublication of the index to a most ambitious work, the *Theatrum Botanicum*, of which Book I, treating

"grasses," was the only part that was complete at the time of his death, and which was actually published in 1658 by his son. There is also a *Prodromus Theatri Botanici*, published in 1620, including only preliminary descriptions of the undescribed species detected by Bauhin during his long botanical career. The three works together are an excellent source of information on the status of the generic concept at the beginning of the seventeenth century.

Bauhin's *Pinax* says that Dioscorides and Pliny made four genera of grasses, whereas later botanists made many. These later "genera," to take a couple at random, are such as the following: *Gramen caninum* (comprehending species that Linnaeus later put into *Triticum*, *Poa*, *Agrostis*, *Aira*, and *Cenchrus*) and *Gramen junceum et spicatum* (including Linnaean species of *Festuca*, *Aira*, *Juncus*, *Scirpus*, *Carex*, and *Triglochin*). Such genera are not so good, on the whole, as some of Bauhin's predecessors nearly a hundred years before would have made, and the generic concepts and nomenclature have become vastly complicated, but we must bear in mind that Bauhin was primarily indexing rather than reforming. Taking a typical case, that of *Cyperus*, he says that the species may be bitter, or they may be sweet (and edible). A bitter *Cyperus* may be either odorous or inodorous, and some part of it may be either round or long. So he divides *Cyperus* into five genera, with the polynomials *Cyperus rotundus odoratus*, *Cyperus rotundus inodorus*, *Cyperus longus inodorus*, and *Cyperus esculentus*. The assemblage as a whole includes a medley of types, Linnaean species of *Cyperus*, *Carex*, *Schoenus*, *Scirpus*, these all *Cyperaceae*, but with them also *Dorstenia* in the *Moraceae*. Obviously there was only a vague idea of any morphological criterion of a genus in Bauhin's mind. As to his nomenclature, there are many instances, perhaps a majority, in which the generic name is incorporated at the beginning into the name of the species, as for instance, most of the species of the genus *Gramen caninum*, two of which are *Gramen caninum, supinum minus*, and *Gramen caninum maritimum spicatum*. Another species of the same Bauhinian genus, however, is *Gramen murorum radice repente*. Here there is nothing in the name to indicate that the plant belongs to the genus *Gramen caninum*. Then there are many instances in which the name for a segregated genus is a condensation of the polynomial name of a species. Thus the two species of the genus *Cyperus esculentus* are *Cyperus rotundus esculentus angustifolius* and *Cyperus rotundus esculentus latifolius*.

The casual reader of Bauhin might too hastily conclude from the chapter headings that his real genera were not the groups, often with binomial and trinomial designations, which are divided into numbered species, but rather the larger categories with monomial designation that head the chapters. It is quite true that some of the genera do indeed have one-word

names, which are used also as chapter headings, but more often this is not so. For instance, Bauhin says that it is possible to reduce the orchids to the five genera which he calls (1) *Cynorchis*, including a subgenus (although he nowhere uses this term) *Cynorchis militaris*, (2) *Testiculus morionis*, which he immediately changes to *Orchis Morio*, (3) *Orchis foetida*, (4) *Orchis Serapias*, and (5) *Testiculus odoratus*. By the time he gets to the actual treatment of the fifth it appears as *Monorchis et Triorchis*. Aside from a few specific names that begin as we would expect with the generic name, we find some species under each whose long names give no clue to the genus under which they are placed. Thus under *Cynorchis* we find names beginning with *Orchis* and *Chamaeorchis;* under *Orchis Morio* are *Orchis flore nudi hominis effigiem repraesentans, mas* [*et foemina*] and *Orchis flore simiam referens;* under the genus *Orchis foetida* are species with names such as *Orchis odore hirci minor;* under *Orchis Serapias* no names begin thus; under *Monorchis et Triorchis* (treated, if we may judge by the numbering of the species, as a single genus) the specific names begin with *Orchis*, *Triorchis*, and *Chamaeorchis*.

In the work of Caspar Bauhin, therefore, the generic concept in botanical classification has become almost wholly divorced from language. The names of species need have nothing whatever to do with the genera to which the species belong. Not one of the phrase names which he retains or proposes for the species of *Curcuma* refers to the genus, and such as *Cyperi genus ex India* and *Crocum indicum proposuit Garcias, foliis milii majoribus: et Acosta, foliis Orchidis Serapiae dictae majoribus latioribusque*, give an altogether wrong indication of relationship, for a *Curcuma* can neither be a *Cyperus* nor a *Crocus* according to Bauhin's own classification. The name of a species by Bauhin's time has become something that need not indicate any genus and may even indicate a genus from which the species is excluded. A name is merely a name, not necessarily indicating generic affinity at all, and knowing where species belong has become merely a feat of memory. Truly simple generic grouping, as found in folk botany and reflected in language, had been lost, by the time of Bauhin's *Pinax*, in a maze of complexity and obscurity.

Matters did not greatly improve until drastic reforms were instituted by Tournefort about 1700. He restored the generic concept to simplicity and utility, and in conventional botanical history is the originator of genera. Of course he was not, but he certainly wrought a revolution in the jumbled botany that he found, turning chaos into order.

From the fact that Tournefort referred all the plants he knew to definite genera, it might be assumed that he had a well-defined underlying philosophy which enabled him to judge of what constituted a genus. He did have, and it is worth while to look into it, as he expounded it in the

famous *Isagoge in Rem Herbariam* which forms the introduction to his *Institutiones Rei Herbariae.*

In the first place he shows that plants generally have roots, stems, leaves, flowers, fruits, and seeds. There may be other parts, and at least five may generally be considered in establishing a genus, for most plants have that many, although some lack stems, some lack leaves, and some lack flowers.

It is of no use, he says, to require close correspondence in as many as five parts, in the species of a genus. There are not many genera with species closely similar in roots, leaves, stems, flowers, and seeds. For instance there are species of *Ranunculus* with tuberous roots, others with fibrous, still others with grumose. The leaves of species in this same genus resemble those of *Aconitum*, of grass, of rue, or of other plants, so one cannot even demand correspondence in four parts.

Suppose correspondence in only one part is required. Then, he says, we can't often arrive at good genera. The leaves alone would not do as a criterion, for then to *Plantago* would have to be added all the plants with leaves like those of plantain, such as the genus *Plantago aquatica*, and the species *Ranunculus Plantaginis folio.* (Note that Tournefort keeps binomial generic names, such as *Plantago aquatica* (now *Alisma*), *Lilium Convallium* (now *Convallaria*), *Primula veris*, *Ruta muraria*, and a few others.) Such a genus as *Plantago*, defined by leaves alone, would make botanists laugh, Tournefort says. So would one based upon leaves like those of *Aconitum*, for it would contain species of *Ranunculus*, *Geranium*, and other genera. Flower form alone as a criterion would be no better, for then, he observes, we would get a jumble of such things as *Cucurbita*, *Convolvulus*, and *Campanula* in the same genus; nothing could be more inept than such a composite. Likewise all the umbelliferous plants would fall together, and an equal infelicity would result from dumping into one genus all plants with papilionaceous flowers. Without laboring through this part of his argument further we may state his conclusion that similarity in two or three parts is all that is generally necessary.

Next he proceeds to show that roots and leaves together will not suffice, nor roots and flowers, nor roots and fruits. However, similarity in flowers and fruits will make the best criterion of a genus. This conclusion he proceeds to justify by saying that no one who looked at it in flower and fruit could deny the name *Viola* to *Herba Trinitatis* of Fuchs. The lack of conformity of its leaves and stems with those of *Viola vulgaris* need not disturb us, any more than the conformity of the leaves of the latter with *Asarum* would lead us to put it into the same genus with *Asarum.* He depends upon conformity of flowers and fruit as the basis for deciding what shall go into *Viola*, not leaves and stems, as Caspar

Bauhin does in the *Pinax*. "Good God," says he, "what a lot of things have come out of Africa in the last few years, in their foliage looking like *Malva*, *Alchemilla*, *Myrrh*, *Coriander*, *Aquilegia*, *Uva crispa*, and what not, but every one, by overwhelming consensus of botanical opinion, some sort of a Geranium!"

Tournefort grants that any rule of thumb may be too rigidly applied, however, and so he will make exceptions when he likes, in order to maintain such natural genera as *Castanea*, distinctive by what he calls its echinate calyx. So there will be genera of two orders of distinctness, which he will call genera of the first and second order, respectively. Of the first, defined by conformity of flowers and fruits, *Aconitum*, *Ranunculus*, *Rosa*, and *Viola* may serve as examples. Of the second order an example is *Bulbocastanum*, which differs only in its tuber, he says, from several genera of umbellifers. *Lilium* is maintained as distinct from *Tulipa* and *Corona Imperialis* by its "roots" being made up of scales, whereas the related genera have tunicated "roots." It is necessary to use characteristics derived from the position of the leaves to distinguish *Abies*, *Pinus*, and *Larix*. The tubular peduncle may suffice to separate *Dens Leonis* as a genus from *Hieracium*. As a final example, showing how far Tournefort was willing to go as a generic splitter, putting most moderns to shame, he says that sometimes the bark alone will do as a generic distinction, and he forthwith follows the ancients in setting up *Suber*, the cork oak, as generically distinct from *Ilex*, the live oak, and both as distinct from *Quercus!*

Tournefort expresses his opinion of his English contemporary, Morison, in an ungentle dig when he says that botany is being involved in a new fog by those who maintain that great genera are not to be split into smaller genera, but, rather, are to be divided into minor genera (subgenera). He cites Morison's polynomially designated subgenera of *Onobrychis*, namely, (1) *Onobrychis scilicet siliquis articulatis et asperis*, (2) *Onobrychis siliquis echinatis, cristatis et spicatis*, and (3) *Onobrychis siliquis echinatis, sed in capitulum congestis, Platani pilularum modo*. Of what use, he asks, is a name which has to do service for such diverse things? If his own definitions are too narrow, if, for instance, someone protests his definition of *Mandragora* on the ground that it requires that *Mandragora* have a monopetalous (i.e., gamopetalous) corolla, whereas there is a polypetalous *Mandragora*, he retorts that if such a polypetalous plant occurs there is no doubt that a new genus ought to be established, as he has often, in fact, established other new genera.

Tournefort's idea of the full names of species of plants is of no little interest. He says they are, after a fashion, definitions. First comes the name of the genus, and then the words expressing the distinctions of the

species. As we have seen, he carries on some old binomial generic names, but most names of genera are single words. He commends Caspar Bauhin for certain neat, brief, elegant, euphonious specific names that better invite to the study of plants than repel. Such are *Ranunculus nemorosus vel silvaticus, folio rotundo,* and *Ranunculus pratensis erectus, acris.* To be condemned, he says, are Morison and Breynius, whose specific names can hardly be uttered with one breath, and go two or three times across the printed page. One excellent reason for small genera, Tournefort says, is that the concept of the small genus comprehends more that is common to all the species, so that the names of the latter may be brief and sonorous. Better to propose new genera with audacity than to force species into places where they do not fit. If genera thus constituted for single species appear superfluous, don't worry about the matter; exploration will sooner or later turn up others.

Tournefort's ideas of genera were clearly pragmatic in the extreme. If new generic names would be conducive to understanding the nature and affinities of plants, he had no scruples about establishing them. Nevertheless he did not do so thoughtlessly or without good reason. His criteria were generally well considered, and few of his generic propositions failed, in the long run, to win the approval of Linnaeus and his successors.

Linnaeus wrote of Tournefort's contemporary, Father Plumier: "Standing forth among all travellers as the greatest, he discovered more than 900 new plants and referred all of them to definite genera. Would that we could have more Plumiers!" This was in reference to Plumier's *Nova Plantarum Americanarum Genera,* of 1703, and is almost the only reference to genera in the *Bibliotheca Botanica* of Linnaeus.

Linnaeus generally accepted the genera established by Tournefort and Plumier, and gave all genera single names, generally very well chosen. Apropos of names, in his quaint classification of botanical authors, he provided for "Nomenclatores Criciti," those who would teach how to construct generic and specific names correctly. Of these useful persons he admitted that none had yet written on this subject and then modestly listed himself as the only one there was! The sweeping reform of nomenclature which he later initiated more than justified his confidence in himself.

In Linnaeus' *Fundamenta Botanica* he laid down the fundamental principle that the genus and species are entities of nature. This conception has been denied by some, but it has clearly been and still is the basic belief of most systematic botanists. It guided Tournefort, then Linnaeus and his followers in grouping as genera those species of plants which seem most similar to one another. Close morphological similarity, in fact, was interpreted by Linnaeus as signifying real genetic relationship. He said himself that no true genus was other than a natural genus, and he even-

tually proposed a theory by which he brought into logical agreement two at first glance incompatible beliefs, that plants are all interrelated by descent, and that species were produced by special creation. I have elsewhere called attention to the curious doctrine, which Linnaeus made public relatively late in his career, according to which it was postulated that fundamentally distinct types, produced in the beginning by fiat, hybridized by miraculous intervention in an orderly manner in all possible combinations, which process was repeated by the primary hybrids and then again by the secondary, until the genera and the species were produced. He said that the morphological combinations, if botanists were keen enough to interpret them, would indicate the true genera. We must recognize that Linnaeus was a forerunner of Darwin to the extent that he believed in the relationship of species and genera by descent.

The constantly more refined methods of systematic botany and the doctrine of evolution, toward which Linnaeus groped, have given new meaning, since the publication of Darwin's epochal *Origin of Species*, to the Linnaean conception "entity of nature." Nevertheless, the majority of modern systematists, still mainly concerned, as Linnaeus was, with morphological criteria, continue to approve the generic concepts of Linnaeus. He himself, approving in general the concepts of Plumier and Tournefort, by the uniform application of the binomial system, restored to Latin botanical nomenclature the simplicity and intelligibility of common speech. Forgetting that large genera may be quite as truly "entities of nature" as small ones, some modern botanists are making far too fine generic segregations, in violation of evidence that too many basically different words for similar things cannot be borne in mind and fall into disuse, and that from a practical standpoint too many names and too many genera obscure rather than elucidate relationships. Just as we quite naturally accept the conclusion that the concept of genus in folk botany was often too broad, and had to be narrowed, so it is quite inevitable that botanists shall continue to accept new generic segregations whenever it appears from increased knowledge and new appraisal of characters that old genera are not natural entities. But that there is any need for a general change in the generic concept, from the standpoint of inclusiveness, we may deny. A large genus may be quite as "natural" as a small one, and from a practical and linguistic standpoint may be a far more useful concept.

ANN ARBOR, MICHIGAN

II. A Survey of Modern Opinion

EDGAR ANDERSON

When I was originally asked to speak on genera from the viewpoint of cytogenetics, I replied that on this problem genetics could contribute nothing and cytology very little. The chief technique of genetics is to cross individuals and from the appearance of their progeny to make inferences as to the germplasms of the two individuals. Very few genera can be crossed and no exhaustive studies of the progeny have been made in the few exceptional cases which were semi-fertile. The chief technique of cytology is to make direct observations on the germplasm. This technique is obviously applicable to the study of generic differences but to yield significant results it would have to be applied in various families of the flowering plants and completely correlated with a taxonomic investigation of the same genera. Most of the cytological evidence compiled up to the present time has been assembled by cytologists who were quite innocent of any taxonomic training or insight and their data cannot therefore be used for this purpose. The few projects which are now under way (notably those of Babcock and Stebbins, 1937, on the Crepidinae and Clausen and Keck, 1933, on the Madinae) are as yet too incomplete and too restricted to permit effective generalizations.

Since, for the above reasons, it seemed to me that genera could not be discussed from the viewpoint of cytogenetics, I asked to be allowed to investigate them in another way. We may think of genera in two quite different ways, (1) as biological units, that is as gross discontinuities in organic nature, or (2) as cataloguing devices used by systematists. These two concepts are overlapping. Such a distinction may even be unwelcome to many biologists; it will, however, be a useful expedient in the following discussion.

It seemed to me that if one could not yet investigate genera as they may or may not exist in nature, he might at least learn something about them *as they exist in the minds of taxonomists.* This I set out to do by framing a questionnaire which would indicate something of the differences of opinion among modern taxonomists. With the help of preliminary discussions with Dr. J. M. Greenman and Dr. C. L. Hitchcock (who are, however, to be absolved from any responsibility) the following questionnaire was prepared and sent out to fifty taxonomists with whose work I was personally acquainted. The list was representative and for reasons which will be apparent below, was purposely devised to include monographers, plant geographers, and students of floristics.

For the symposium on Genera I am attempting to find the opinion of present day taxonomists. Will you, therefore, be kind enough to fill out the following questionnaire? A stamped, addressed envelope is enclosed for your reply. If you are unable to fill out the questionnaire will you at least indicate here your reason for not doing so?

( ) I am too busy. ( ) I feel the questions are trivial.
( ) I am out of sympathy with any such investigation.

Question No. I.

Which in your opinion is the more natural unit among the flowering plants, the genus or the species? (i.e., which of the two more often reflects an actual discontinuity in organic nature.)

( ) The genus is the more natural unit. ( ) The species is the more natural unit. ( ) I have no opinion on the subject. ( ) I think the question as phrased above is meaningless. ( ) I do not understand the question as phrased above.

Question No. II.

If genera are more clearly marked than species this may be due to either or both of two quite different processes: *A*. Genera may originate in the same way as species and achieve their greater distinctness by the disappearance of more intermediates. *B*. Genera may originate in a different way from species; i.e., it is conceivably possible that there are different forces which have operated in the origin of genera. If *"A"* has been the chief method by which genera have originated then the morphological differences between genera, though greater than those between species, should be the same *sort* of differences. If *"B"* has been the chief method then we might expect generic differences to be of another kind from specific differences. In the light of the above discussion will you indicate your opinion below? Check more than one space if you wish.

( ) Generic differences are of the same kind as specific differences though they may be greater. ( ) Generic differences are of a different kind from specific differences. ( ) I have no clear opinion on the subject. ( ) I do not think the statement has any meaning. ( ) In my opinion the statement is obscure.

Question No. III.

In an attempt to avoid misinterpretation the same idea has been phrased in another manner. Please check your reaction to the following statement: Generic differences could be compounded from specific differences.

( ) Yes. ( ) No. ( ) Question meaningless. ( ) Question obscure.
( ) No opinion on the subject.

To those who care for it a tabulated summary of the replies will be mailed. If you would like such a summary please make a check in the following space ( ).

The response to the questionnaire was most gratifying (Table 2). Practically all in the group checked their responses and a considerable number amplified the questionnaire with a discussion of the points which had been raised. It was immediately apparent that there was a very considerable relation between interest in the questionnaire and the age of the person replying. Among the younger men such expressions as "I am looking forward to this symposium" or "I have discussed your questions at length with such and such a colleague and they have stimulated an interesting discussion" were common. Many of the older botanists, on the other hand, answered with reluctance or expressed doubt as to the wisdom of the enterprise. By grading interest in four objective classes it is even possible to demonstrate this correlation in tabular form (Table 1). It is one

TABLE 1

Correlation between interest in the questionnaire and the age of those replying.

	UNDER 40	40 TO 55	OVER 55
Not in sympathy with questionnaire	..	..	2
Replied without comment	2	7	7
Replied with additional comment	6	6	5
Replied and also expressed interest in questionnaire	12	1	1

thing to demonstrate a correlation and another thing to interpret it correctly. In this case several factors are probably responsible for the correlation. Certain of the younger men might have been deferential towards the project, since I was older and presumably wiser. And for the same reason those older than I might have had less tolerance for a novel project by a much younger man. It is also undoubtedly true that the genus problem is so complex, and requires such a long apprenticeship, that few young biologists have enough experience to discuss it intelligently. The older men were experienced enough to realize this fact and to realize the complexity of the problem. One of this group wrote me as follows, and I quote his remarks because I find myself very much in sympathy with this point of view: "Your circular letter of August 26th does not arouse any warmth within me. All the questions you raise are purely speculative, and in the present state of our knowledge they cannot be answered. These problems work themselves out practically for each publishing taxonomist, and a

fair agreement has been reached as to the limits of genera and the limits of species without much reference to philosophical considerations. Discussion of such problems is likely to be made by persons who have no taxonomic training and the conclusions would be of little practical value. Probably I should not take the time to read them. Persons who have no actual contact in the diagnosis of species are likely to want definitions of what a species is. The taxonomist does not raise the question in that way, but meets each case as it come to him. Perhaps in a century or so from now we shall be able to approach such problems with sufficient knowledge to make the conclusions significant."

TABLE 2

Summary of 48 replies to questionnaire.

QUESTION I

Genus the more natural unit	26
Species the more natural unit	8
Sometimes one, sometimes the other	11
No opinion	1
Question meaningless	2

QUESTION II

Genera originate in the same way as species	31
Genera may originate in a different way	4
Genera may originate in same or in a different way	9
No opinion	4

In my opinion there is another, and more important reason for the correlation between age and interest. Many of our younger taxonomists have a different biological training from the older generations. Consequently they have a different attitude towards taxonomic work and that difference is reflected in the correlation shown in Table 1.

A large proportion of the replies warned me that I would find great differences of opinion on these questions. In the face of such statements it is particularly interesting that of the fifty replies received twenty-one were absolutely identical. A considerable proportion of the remainder differed only in one detail or another. Apparently therefore there is more agreement among modern taxonomists than they themselves realize. This orthodox point of view revealed by the questionnaire is that genera are on the average more natural units than species, that they originate in the same way as species and that generic differences could be compounded from specific differences.

The replies were then studied to see if there was any obvious correlation between the above point of view and the experience of the botanists who held it. Since there seemed to be a connection between monographic experience and "orthodoxy" an attempt was made to group the replies with

reference to the monographic experience of those replying. For this purpose it would have been ideal to have had twenty-five replies from botanists who had done nothing but monographic work and twenty-five from those who had done no monographic work whatever. Unfortunately there was no such clear cleavage and we had to content ourselves with selecting the following two groups, which have been called "monographers" and "non-monographers" to simplify Table 3 and its discussion. It would be more truthful to refer to the first group as "taxonomists whose experience has been rather exclusively in monographic work" and to the second as "taxonomists who are not monographers or who have had extensive experience in other biological disciplines."

Group I. "Monographers."

Blake, Epling, Fosberg, Gleason, Goodman, Greenman, Hitchcock, Hopkins, Johnston, Kearney, Munz, Ownbey, Pennell, Rosendahl, Sherff, Wright Smith, Lyman Smith, Svenson, L. O. Williams, Woodson, Yuncker.

Group II. "Non-monographers."

Anderson, Babcock, Camp, Cory, Deam, Hermann, Howell, Kinsey, Mattfeld, Merrill, Muenscher, Müntzing, Nelson, Palmer, Raup, Stebbins, Steere, Steyermark, Stockwell, Weatherby, Wiegand.

The replies of these two groups are tabulated in Table 3. It will be seen that even though the distinction between the two groups is somewhat imperfect there is a decided correlation. Two-thirds of the monographers are "orthodox" but less than one-third of the non-monographers.

TABLE 3

Correlation between monographic experience and "orthodox" opinion in regard to genera. Further explanation in the text.

	UNORTHODOX	ORTHODOX
Monographers	14	7
Non-monographers	6	15

SUMMARY

It should again be emphasized that the results of this investigation have probably little or no bearing on the question of genera as they may or may not exist as evolutionary units. The aim of the investigation was to ascertain something about genera as they exist in the minds of taxonomists. For a representative group of 50 taxonomists the following facts were established.

(1) There is a perceptible correlation between age and interest in discussing such concepts as genera. In part, at least, this probably reflects a

changing attitude towards taxonomic work. (2) Nearly one-half of those interviewed gave identical replies to the whole set of questions. (3) There is a very strong correlation between monographic experience and the tendency to the point of view that genera are more natural groups than species, that they originate in the same way, achieving their greater discontinuity by the disappearance of more intermediates.

CONCLUSIONS

The results reported above and the various comments, which accompanied the replies, lead me to conclude that much taxonomic work is strongly colored by a widely accepted hypothesis. The notion that individual differences are gradually built up into varietal, and these progressively into differences of specific and generic rank is so logical that it has, consciously or unconsciously, been accepted by many taxonomists as absolute dogma. More than one systematist in replying to the questionnaire expressed astonishment that one might even consider evolutionary forces which would lead to the separation of genera but which would not operate in the formation of species. Yet by experimental analysis we already know of various quite different isolating mechanisms of evolutionary importance (Dobzhansky, 1937). It is scarcely credible that there are not others still to be discovered. We already know of mechanisms which may operate in the deployment of subgenera but may not in the deployment of species. It is already possible to indicate species which are separated by evolutionary forces different from those forming varieties within the same species (Anderson, 1936). The patterns of evolution are too complicated and too various for the universal application of any simple phylogenetic hypothesis.

For such reasons as these I find myself in sympathy with those who dissented from the "orthodox" view reported above. In my opinion it would be well if monographers could approach their work with minds unprejudiced by evolutionary theories. We are so certain of the fact of evolution that we are prone to forget how little we know about the forces behind it. Personally I find myself in complete agreement with the following comment which was appended to one of the replies.

"It looks to me as if you were trying to generalize on the assumption that there is a basic uniformity in taxonomic groups. There is nothing of the sort. Taxonomy is only a glorified guess—an attempt to construct a cross-section of lines of descent in a form intelligible to the human mind. It always contains two variable quantities—the plasticity of animate nature and the differing points of view of the people who work at it. You can generalize successfully, if at all, only by keeping these facts constantly in mind. I suspect that the situation is best expressed by the old aphorism:

the only general rule is that there is no general rule. Therein lies the fascination of taxonomy for those who like it. It is not a matter of mechanically applying a universal set of categories to given groups of facts. Each group one tackles presents a fresh and original problem; for each, one has to work out anew the method by which he may best achieve that transforming of confusion into order which is the great satisfaction of pure taxonomy."

NOTE:—When replies to the questionnaire arrived, I realized that there had come into my keeping, material which was of extraordinary biological interest and which would be of increasing importance in the future. I am accordingly having the replies bound, together with their accompanying letters, and deposited in the library of the Missouri Botanical Garden.

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III. Genera from the Standpoint of Morphology

J. M. Greenman

My concept of the genus has been formed through a practical experience in the field of taxonomy extending over a relatively long period of years. It has developed gradually, but it was first formulated when influences brought to bear were on the whole conservative. I learned from my teachers of biology, from my associates, and from my own observations, that a genus is a taxonomic category consisting of one or more related species, and that a group of allied genera constitute a family.

In simple terms then, but in degrees of diminishing importance, there is the family, the genus, the species, and the variety. Other categories may be interpolated if thereby clarity and convenience be enhanced.

Thus, classification is fundamentally a practical arrangement for convenience—a means to an end. In other words it furnishes a ready instrument for identifying any given plant and placing it in its proper pigeonhole. Little thought was given to any underlying principle or philosophy concerning the classification. And I fancy that some botanists of today look upon classification, or taxonomy, as being only such a mechanical device. The basis of our present system of classification is quite another thing, and it is of fundamental importance. It is the result of the experience of many generations; and it rests primarily on comparative morphology. Moreover, there is a definite philosophical principle underlying the system, namely, the arrangement of the larger categories in such a manner as to indicate, through comparative morphology, their genetic relationships and to some extent their probable phylogeny.

No one now claims, no one has ever claimed, that the present system of classification, namely, the one elaborated by Engler and Prantl, is perfect and final; but, that on the whole it expresses better than any other system of classification previously or since proposed a relatively natural grouping of plants in accordance with our present knowledge of them.

Of the taxonomic categories mentioned above, namely, family, genus, species, and variety, each category may vary to a considerable extent in accordance with individual interpretation. That is the personal element which has always been a factor and probably always will be so long as the subject remains a dynamic one; but, even so there is almost always a universal understanding as to what is meant by a generic category.

However, it is important to bear in mind that the concept of the genus, as well as the species, may vary not only with the individual's interpretation, but it may vary more or less in accordance with the trend of the

times. This is perfectly natural, since we are all influenced to a greater or lesser degree by the opinions of our contemporaries.

At the present time taxonomists are working almost universally in accordance with the type-concept idea. That is, the species of a genus must conform in all essential morphological characters to those of the type-species of the genus under consideration, and similarly all members of a species must conform in the essential morphological characters to the type-specimen of the particular species concerned.

In the absence of a type-specimen, that is where there is no historical type extant, a standard-species may be substituted. Likewise in the absence of a historical type specimen of a given species a selected specimen may be taken as typifying the species. In accordance with this plan of operation, the generic concept centers around a concrete thing—the type-specimen. Whereas, formerly the generic and the specific concept centered around the complex which represents the genus or species in its general area of distribution, and more particularly the dominant form.

To show this change in concept, may I refer to an incident in my own experience (if you will pardon a personal reference). Some years ago, when I was a graduate student working under the direction of Professor Adolf Engler in Berlin, I recall very well one of the many discussions which took place during the lunch hour. The late Professor Ernest Gilg said to me, "Aber, Herr Greenman, was meinen Sie ueber das Wort Type oder Typus? Meinen Sie viellicht das Original?"

At that time in many of the great botanical centers in Europe and elsewhere the type-concept centered around the most common representative of the genus, as well as the species, in its total area of distribution rather than on the historical type. Again may I say that it becomes necessary to bear in mind the time factor involved when we try to interpret the delimitations of a genus or of a species?

Many genera, as now delimited in literature, have been greatly altered from the original interpretation placed upon them. Some of the older and larger genera now include many generic synonyms. Take for example *Andropogon*, *Panicum*, *Crepis*, etc. It not infrequently happens that generic names, which have been reduced to synonymy, upon a more intensive restudy have to be revived and given coordinate generic rank. This was shown to be the case with *Astranthium*, a genus proposed by Nuttall and reduced to synonymy under *Bellis*, but upon restudy by Esther Larsen (1933) it was revived and reinstated as a valid generic entity.

Another instance is that of *Youngia* of Cassini, a genus which was regarded for many years as synonymous with *Crepis*, but upon an intensive restudy by Babcock and Stebbins (1937) it has been reinstated by them as a valid genus.

I mention these examples, because it is impossible to treat all genera in exactly the same way; not infrequently are they differently constituted, and must be treated accordingly.

Apropos of the lack of uniformity in genera, may I say that new genera have been proposed in the course of studies made on the flora of a limited region; and while it is true that such genera appear to be amply distinct when compared with other genera of the same region, yet when studied in relation to the entire representation of the genera concerned, the newly proposed entity is not infrequently found to be merely a variation. Hence, it is very important in formulating our concept of a genus, and of a species also, to take into consideration not only comparative morphology, but also geographical relationships. This principle, I think, has been well demonstrated by Dr. H. K. Svenson in his work on *Eleocharis*.

Much has been said about the segregation of genera. I am not opposed to segregation if it can be justified on the basis of comparative morphology, including characters not previously recorded, and the application of any supporting evidence obtained from anatomical studies, cyto-genetic investigations, or any other sources of information. We should recognize the desirability, however, of keeping the generic category as uniform as possible.

Unless some very definite object is attained by segregation of relatively homogeneous groups of plants, such for example as *Aster*, *Erigeron*, *Conyza*, *Baccharis*, *Senecio*, *Euphorbia*, and *Cassia*, I am personally inclined to think that it is more practical to retain these groups in their traditional sense. Certainly such a treatment is less disconcerting to botany in general than to make numerous possible changes. Generic segregation almost invariably means the introduction of new combinations and new names.

After all *Aster*, *Erigeron*, *Conyza*, and *Baccharis* are not entirely and mutually exclusive categories, any more than are *Cirsium* and *Carduus*; since, when one studies large series of specimens representing these genera, it is manifest that they grade imperceptibly one into another. But largely for the sake of convenience they are maintained as separate genera.

If one began to segregate the genus *Senecio*, as it is usually interpreted, it would be possible to recognize some twenty or more genera in which habit would play a prominent part. Difference in habit is due primarily to change of environmental conditions. And when one studies this genus throughout its entire geographical range, which is not exceeded by any other genus of flowering plants, it would be exceedingly difficult to maintain the possible generic segregates. Furthermore, the number of new names and new combinations would be excessive and confusing.

On the whole, therefore, my personal inclination is towards a conservative concept of the genus and the retention of well-established generic names in so far as consistent with the comparative morphological characters originally ascribed to them, especially when corroborated by additional knowledge gained by a more intensive study resulting from improved technique and new methods of attack.

Finally, may I say that while I am of the opinion that comparative morphology must remain as the fundamental basis of classification, yet I welcome the important contributions to taxonomy, which have been made through cyto-genetic studies and experimental investigations.

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IV. The Delimitations of Genera from the Conservative Point of View

Earl Edward Sherff

It may seem presumptuous to attempt to represent within twenty minutes, even in small part, the conservative school of thought in plant taxonomy. In fact the term conservative itself has been sadly abused and one doubts if its definition for botanists generally is not largely subjective and dependent mainly upon who does the defining. By one writer conservatives have been characterized as those seeking relationships and hesitant to describe new species, while radicals are characterized as being impressed by diversification and anxious to record their findings. But with many of us the distinction seems akin to that made long ago between orthodoxy and heterodoxy, namely, that orthodoxy is my "doxy" and heterodoxy is yours. Certain it is that some taxonomists have professed a conservative viewpoint for generic delimitations and then, by utter disregard of nomenclatural rules or taxonomic precedent, or both, proceeded to make wholesale changes or innovations of nomenclature in other respects, sometimes going farther than even a self-respecting radical or liberal would feel warranted in doing. Thus, for example, what amounted almost to an obsession with one of our late American workers in taxonomy was the designation and naming or renaming of subspecies, by which he meant commonly nothing more or less than the conventional varieties as they were understood by Linnaeus, Augustin DeCandolle, Willdenow, Gray, and a long line of other workers. If we are to accept the principle of a binomial nomenclature at all, it would seem self-evident that we should not only abide by the rules adopted by our international congresses but also, wherever an arbitrary choice is to be made, defer to the carefully reasoned practices and matured judgments of taxonomy's founders, whenever these practices and judgments do not conflict with present-day rules.

Both radicals and conservatives must use the binomial system of nomenclature. An essential feature of this system is, of course, that the binomial for any species derives its first part from the generic name. This feature has been lamented as a fundamental weakness of the binomial system, since a change in our conceptions of genera and species eventuates frequently in a change of the scientific names. L. H. Bailey even states that "we should have gained much in simplicity of literature, in clarity and in popular usage, if we had had a mononymy or other arrangement instead of a taxonomic dionymy." Even admitting the truth of this statement, should we not have lost immeasurably had nomenclature failed to asso-

ciate for us, as it attempts to do under the binomial system, related specific entities under one generic name? In any event, as long as the binomial system of nomenclature is officially used by all of us, truly conservative botanists will be reluctant to recast generic concepts or limits except upon the most convincing evidence.

Conservatives, generally speaking, attempt to delimit genera with approximately the scope employed by Tournefort and later by Linnaeus. To sneer at our inability to define categorically what is meant by the Linnaean concept of genera is beside the point. True, there has been inconsistency, but it likewise is true that an unbiased study of Linnaean genera usually imparts a *genus sense* which is not far off the middle road of taxonomic opinion. Apparently much of the mischief done heretofore in carelessly juggling generic limits must be blamed upon certain viewpoints and procedures which the conservatives must condemn if they are not to condone the mischief itself. May we mention a few of these very briefly.

First there is the loose talk heard in some quarters about cumbersome trinomials and quadrinomials. In case a cosmopolitan or at least polydemic species exhibits several varieties and forms or *formae*, we are in effect told to elevate each to specific rank and thus simplify our nomenclature. A logical outcome of such a course, however, is sure to be the warping of our *specific* concepts far past the limits understood for species by Ray or by Linnaeus. In short, we shall have a degradation of the original species concept in numerous cases but its retention undisturbed in the others. Some of our so-called radicals, having committed themselves to this way of doing, have awakened to find too many species in some of the genera. They have then made generic segregations to ease the fancied tension from within which they themselves had helped to create. If we are truly enamoured of conservatism and genuinely believe in a logical delimitation of genera, we must not neglect our *species* concepts.

Another matter that must engage our attention is the provincialism that has flavored all too much of the work on the manufacture of new genera. The entire earth must be taken as the source-book of our generic concepts. The writers of some of our manuals and local floras have overlooked this fact. Many times they have erected so-called new genera largely or solely upon the basis of the species within their own geographic range. A classic instance is that of *Astragalus*, where the author of a manual covering part of western North America decided to employ eighteen distinct genera instead of one. But, as Skottsberg, a distinguished representative of conservative opinion abroad, points out, *Astragalus* is not exclusively or even mainly a North American genus. "Is it likely," he asks, "that the eighteen United States genera will be left untouched and natural after

the 1,000 non-American species have been taken into due consideration?" Skottsberg sets forth additional examples, one of them that of *Vaccinium* as treated in American manuals. For the American species, the keys to the sections *Vaccinium* proper, *Cyanococcus*, and *Vitis-Idaea* are sufficiently diagnostic. When, however, a half-dozen mutually close Hawaiian Island species are compared with the same keys, they are found to run to different sections, or indeed to possess overlapping characters. A believer in small genera might here be inclined to put *Cyanococcus* and *Vitis-Idaea* as separate genera and erect one or two additional but tiny genera to take care of the Hawaiian misfits. A conservative course would doubtless be, on the other hand, the continued maintenance of the genus *Vaccinium* in its broader sense, coupled with a redefinition of the component sections. A point to be emphasized, however, is that the author of a local flora or a manual for a restricted range is many times unfamiliar with a considerable percentage of species in the genera treated. In most cases the presumption of evidence will be against him. The least he can do and at the same time show respect for other workers who must use his book is to refrain from altering the status of any genus unless he has a comprehensive monographic knowledge of it for whatever parts of the earth it may inhabit.

A third matter, one closely related to the second, is the need for greater emphasis upon monographic research. It may be true, as some able workers assert, that various large genera like *Opuntia* and *Euphorbia* need breaking down into smaller units if we are to have a genus concept such as Linnaeus would have formulated could he have had all the information that we possess today. But only extended and painstaking monographic research will be of much value in helping us to make the appraisals or evaluations needed for settling these cases. May I inject here my own personal conviction, intensified during several years' monographic research upon the genus *Euphorbia* as it occurs in the Hawaiian Islands? I recognize of course that a large genus may embrace species more diverse morphologically than species of many admittedly distinct Linnaean genera. Such a genus is apt, however, to display within itself such a profusion of intergrading and overlapping characters as to make clean-cut generic segregations, at least within our present geological era or epoch, quite impossible. Conservatives are stigmatized as inconsistent if they move slowly in accepting some of the proposed segregations. But of what use is it, we may well ask, to reach for imagined increase in consistency if in so doing we throw the species into such confusion that no honest student can successfully fit to them our binomial system of nomenclature.

The conservative's preference in a general way for stability in nomenclature is sometimes criticized as making for stagnation of taxonomic

progress. One botanist has rightly termed the hope for complete stability a "will-o'-the-wisp calling us to the swamp of unattainment." But surely no conservative hopes for or expects complete stability. New forms continue to be discovered and, with their study, limits of certain genera may have to be changed. Old genera that have received their present taxonomic identity largely by piecemeal accretions from the pens of numerous authors must needs be restudied monographically. Much has been written about polyphylesis, or the origin of a genus or other group at different places or times by convergence of two or more lines of descent. Little has been written about the *pseudo-polyphylesis* that has arisen sometimes in literature when two or more authors with diverse points of view have referred generically different forms to the same genus. Conservatives, however, should be and doubtless will be as prompt as any others to welcome a re-examination of the morphological and phylogenetic bases on which each such genus rests. They will insist none the less that major nomenclatural changes be made only after extended and detailed research and not as the result of personal whim, or caprice of fancy, or mere love for something new. Probably our present era exceeds all past eras in the tendency to mistake mere change for genuine advancement. The plain duty of taxonomists, whether of the conservative or radical persuasion it matters little, is to shun all change made merely for the sake of change. They must seek an atmosphere of the utmost objectivity for their researches. It would be false to say that our concepts, generic or otherwise, are never in part subjective, but the degree of subjectivity should decrease as the comprehensiveness and thoroughness of our work increase.

A word should next be said against the arbitrary separation of genera, as is still often done, solely upon the presence or absence of one or more supposedly diagnostic characters. Under the theory of special creation this may have seemed justified. But we cannot hope to reconcile our presently held evolutionary theory of phylogeny at all points in the plant kingdom with such a practice. The genus *Cosmos* may be taken as an illustration. If we insist upon the presence of a rostrate achene, as was once done, several undisputed species of *Cosmos* automatically fall out of the genus, among them *Cosmos calvus*. If we insist upon wingless achenes, then *Cosmos Blakei* is excluded. If we demand slender roots, the entire section *Discopoda*, characterized in part by having fascicled, tuberous roots, must be dropped. Yet *Cosmos*, whether we assume for it a monophyletic or a polyphyletic origin, is so natural a genus that it was not even divided taxonomically into sections until 1932. The presence or absence of retrorsely barbed achenial aristae in the separation of the genus *Bidens* from the genus *Coreopsis* offers another illustration. Linnaeus, Augustin

De Candolle, and a host of other workers separated the two genera primarily by this one character. When Asa Gray found a herbarium specimen of the so-called *Coreopsis aristosa* possessing retrorsely barbed aristae instead of the antrorsely barbed ones customary in that species, he designated it "*Coreopsis aristosa* transformed into a *Bidens*." Later he treated this and similar forms in his *Synoptical Flora of North America* as hybrids between *Coreopsis* and *Bidens*. But with the advance of knowledge that came during the decade following the appearance of Gray's *Synoptical Flora*, it became evident that these forms were not hybrids. On the contrary, they were recognized as definite varieties. We then had the anomalous situation in which *Coreopsis aristosa*, *Coreopsis involucrata*, and *Coreopsis trichosperma*—to use the names then accepted for these species—were assigned to *Coreopsis*, while their varieties with retrorsely barbed aristae were to be referred to another genus, *Bidens*, if the traditional basis of distinction were to be observed. N. L. Britton promptly sensed the utter inconsistency and indefensibility of insisting further upon the following of tradition—and here we digress to remark that Britton would rank with most of us as a liberal or radical, not a conservative. Yet the course that he adopted in this and many other instances, when contrasted with that previously followed by some who were professedly conservative, should remind us that not all taxonomic progress has been accomplished or even initiated by the conservatives. With this thought in mind, may I confess to almost an outright fear of doing violence to the interests of plant taxonomy by appearing to divide its devotees for even twenty minutes into two distinct schools of thought? In actual experience there are more than two schools and each school has several grades. Moreover, the enrollment is frequently shifting and sometimes even switching schools. But to return to the case in point. Britton at once referred the so-called *Coreopsis* species exhibiting ambiversalism in their aristal barbs to the genus *Bidens*. In so doing, he was guided not by a single arbitrary or artificial character but by the sum total of characters manifested in each group studied. Such a course, it would seem, conservatives must ever stand ready to adopt if our taxonomy is to take even the slightest cognizance of evolutionary phylogeny.

This brings us to the often heard criticism that considerations of phylogeny will forever upset nomenclature. In the multitudinous cases like those mentioned, however, it will usually be only one or a few of the borderline species that will require shifting and consequently a change in name. The genera themselves will stand largely intact. But even in cases where the supposed phylogenetic record would appear to dictate radical rebuilding of generic concepts or widespread shifting of generic limits, it should be remembered that phylogenetic preachments vary highly

with the one uttering them. They may reflect a complex of emotional, nutritional, economic, and, someone has been cruel enough to add, pathological factors, a complex that has been known more than once to express itself in distinctly different phylogenetic explanations by the same individual within successive periods of time. Here, may I say, all true conservatives should welcome carefully thought out contributions from the standpoint of phylogeny, but we can have little patience with ever-recurrent, petty tampering in generic limits. Especially must this be so if we are led to suspect that a fortnight's sojourn at the seashore or a different brand of breakfast food would have crystallized into a different phylogenetic scheme of relationships. A recent writer has pleaded for a freer use of subgeneric sections to avoid the needless multiplication of genera and consequent alteration of numerous binomials. And indeed it would seem that there is much to commend such a plea, especially for the many cases where equally competent and equally well-informed authorities disagree.

Passing over several additional considerations which are germane to the subject of generic delimitations but which must be omitted here for lack of time, I shall conclude by discussing for a moment the urge made upon us, that we turn to experimental taxonomy, especially in its ecological and genetical aspects. As was pointed out by De Wildeman some years ago and also by Wiegand, the data offered by experimental taxonomy are not usually of practical value to the general taxonomist, even though they are very desirable and often capable of throwing great light upon the significance of morphological characters. To quote Wiegand verbatim, "such data are often impossible to obtain, sometimes because of the unavailability of the living material, sometimes because, as in the case of woody species, the time required to grow the plants is too great, but often also because of the large number of plants concerned." Personally, I would be the last to discourage monographers anywhere from supplementary cultural studies. But if it be admitted that generic characters as a rule are especially well ingrained into the evolutionary fiber of plant species, it would seem that limits of genera, as apart from limits of smaller units, will not soon need alteration because of experimentally adduced evidence. It appears not unlikely that far into the future, as already in the past, we must perforce heed the counsels of morphology and ofttimes of geographic distribution in the delimitation of genera for all unless some of the very lowest plants.

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V. Our Changing Generic Concepts

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So far during this symposium there has been presented a most interesting discussion concerning the concept of the genus. Professor Bartlett, in his inimitable manner, has traced the early history of the concept of this unit of nomenclatural biology. Dr. Anderson, by means of his questionnaire, has collated and evaluated the thoughts and ideas of various of our modern taxonomic workers on the status of the genus. To this much-discussed problem, and based on patient study and much thought, Dr. Greenman has added his personal concepts. And Professor Sherff, using stability as the pillar around which he built his most excellent discussion, has presented a few of the many and valid arguments for the perpetuation of this stability.

It is therefore fitting to remember that the thing which we as taxonomists have been praying for—and even legislating for—is nomenclatural stability. It is the bright star toward which we have been steering; the goal we have been striving for; the haven of dreams come true—where there shall be no more changing of names.

But before I proceed with this discussion it might be well to make a public confession. Surrounded every day by herbarium cases in which repose specimens labeled with more than 150,000 different names, I am opposed to any changes which will necessitate the learning of new ones for the pitifully few of those I do know. At heart, therefore, I am a taxonomic conservative, a worshipper at the altar of nomenclatural stability. But even so, I trust you will permit me my brief moment of intellectual agnosticism while I depart from the broad path of fundamentalism; while I chance the difficult way of the transgressor along the stony road of the one whose assigned task on this program is to discuss, with sympathy, a most unwelcome topic—the splitting of genera.

What the name of an organism might be would make no difference, if it were a name and nothing more; but, under the present system in taxonomy, there is an implied consanguinity, an expression of relationship between species in so far as the generic name is concerned. We find today, therefore, that the genus is less a taxonomic catch-all and increasingly a unit expressive of close phyletic relationship.

Thus, among professional taxonomists, two schools of nomenclatural thinking in regard to generic delimitation have arisen and are now pursuing their own ways. At times during the development of the science these concepts were intertwined, often they ran parallel and, today, some

workers in the one group feel that the concepts of the other are so divergent from a fundamental convenience that they plead for legislative fiat to control their activity. An activity which those who pride themselves on being called conservatives consider as chaos, but which by the others is thought of as scientific progress.

Now, for a moment, let us consider certain of the backgrounds of one of these schools of thought in regard to biological nomenclature. At all times in the present discussion, we must remember that most of the genera around which the present controversy centers were described, and therefore delimited, during that period when biologists held as a basic principle the doctrine of Special Creation and its necessary corollary, the immutability of life forms. The philosophy of those who hold to a traditionally rigid concept of specific and generic delimitation was therefore founded on the basic assumption of a Special Creation. They will deny it, but the evidence is so obvious that they are in error if they try to rationalize their concepts in any other way. We may only hope that they really believe differently.

However, even in the early days, the facts, those insidious things which are continually raising their sinister heads, began staring the fathers of our science in the face and they soon began to be troubled with the knowledge that a nomenclatural unit was a concept and not a fact; that there were no hard and fast lines between the separate entities of each taxonomic category; that not only species, but genera and even families might intergrade. But these things came late in the making of the science and long after the definitions of the classic genera were laid down. I cannot emphasize it too strongly: those who are most intent upon the retention of the nomenclatural *status quo* are, today, confronted with the task of trying to rationalize a static system of immutability with the known facts.

Perhaps the central idea back of this should be expanded, not that all of us do not understand the situation, but merely to put it in a more concrete form. Briefly, our present system of nomenclature, in a general way, is organized on a basis of similarities, having as its fundamental principle a doctrine based upon the thesis that a community of similar morphological structures indicates relationship. With this criterion established, the beginning student of taxonomy soon learns that the species of a single genus have more characters in common than do the sister genera which constitute a family. But as his studies progress, it is not long until he discovers that there is no equality in the standard of delimitation; that in one group of plants, those characters which scarcely constitute specific differences, in another may be sufficient to separate the genera.

For example: in an attempt to rationalize the Vacciniaceae (if I may be permitted to speak of them as a family and not part of the Ericaceae)

I am confronted with the situation of finding, in the classic treatments, that such things as the articulation of the pedicel, which serve in part to separate the genera of the Thibaudieae, are in the Euvaccineae not considered as having sufficient weight to be included as characters separating even the species.

Let us now, for a while, consider another phase of this problem: certain of the goals of taxonomic research. As I have intimated, there are, at the present time, two rather definite schools of taxonomic revisionists. One of these includes those who, in their revisions, follow the already established generic lines, their work consisting in part of weeding out the synonymy that has, perhaps unavoidably, slipped into the literature of the group and also listing or describing the new material found since its last monographic treatment. The other school is not so much interested in the mere cataloging of known species as in a study of the origin, evolution and dispersal of a group of plants. It is this group to which the epithet of "splitter" is most often applied. It can only be regretted that some of the worst offenders in this matter were not so much monographers, but students of regional floras and, although much of their work undoubtedly will be permanent, it serves temporarily, at least, only to becloud the main issues. On the other hand, the honest monographer studying the group on which he is engaged from the standpoint of its total distribution, sees it as a group of plants which are the result of divergent lines that have proceeded out of the world's dim past into the present and knows that the plants in his hands, in themselves, do not constitute an orthogenetic series but are only the ends of a much-branched and often tangled system of descents. The monographer with such a viewpoint is likely to have a vastly different concept as to what constitutes a genus from the one who is merely cataloging the valid species of a group. I have not said that one method is better than the other, nor do I more than intimate that one is to be desired rather than the other. *They are intellectual activities of different sorts and, as a result, their end-products will be different.*

With this in mind and of myself knowing nothing about the mosses, I recently wrote to one of our well-known bryologists[1] for his opinion on what has been happening to the classic genera of bryophytes. I shall quote from his reply:

"There has been a tremendous change in the concept of the genus in mosses and hepatics in the last century. In the time of Linnaeus there were very few genera. Nearly all the acrocarpous mosses were members of *Bryum*, although the atypical and characteristic *Buxbaumia* and *Polytrichum* were, of course, recognized. Almost all pleurocarpous mosses were put into *Hypnum*, although, again, the absolutely unmistakable *Fontinalis* and *Neckera* were even then

[1] Dr. William Campbell Steere.

segregated. In the middle of the nineteenth century, however, a great splitting of the Linnaean and Hedwigian genera was effected in the epochal work of Bruch, Schimper and Gümbel (*Bryologia Europaea*) which was published between 1836 and 1855. The most important splits made here were the recognition in the old genus *Hypnum* of natural groups as new genera, such as *Brachythecium, Amblystegium, Plagiothecium, Thuidium, Pseudoleskea, Heterocladium,* and a dozen others.

"When the Musci of the whole world were evaluated as a group, rather than as an extension of the local flora of Europe and the United States, it was realized that mosses placed closely together in the same family, or even as congeners in the earlier systems, were really far separated. Through the work of Müller, and later Fleischer and Brotherus, whole new families and genera were erected for well known species. Whereas Linnaeus and, fifty years later, Hedwig, recognized a dozen or two genera, the list of valid genera in the last edition of Engler and Prantl (vol. 11: 1925) takes several pages. The tendency now is not so much to erect new genera, but toward a general recognition of splitting done since the turn of the century by Fleischer, Brotherus, Cardot, *et al.* However, I recall a paper by Dixon since 1930 in which he described ten new genera!

"It is therefore obvious that the breakdown in the Musci, insofar as the generic concept is concerned, is general. Now for examples. Perhaps the best are those from well known sources, and so I shall make a few comparisons between the old familiar Grout's *Mosses with Hand-lens and Microscope* (1903), and the newest and best, yet conservative work of Grout (as editor) *Moss Flora of North America, north of Mexico. Dicranum fulvellum* and *D. Starkei* are separated out into the genus *Arctoa. Dicranum longifolium* is now the type of *Paraleucobryum.* Although Grout does not segregate *Dicranum flagellare* and *D. montanum,* many American bryologists call them species of *Orthodicranum.* Still other segregates are recognized by Engler and Prantl. *Funaria* has been split, yielding the genus *Entosthodon.* The old genus *Amblystegium* has been broken up into *Amblystegium* (emend.), *Hygroamblystegium, Leptodictyum,* and *Sciaromium. Calliergon* yields *Calliergidium* and *Calliergoniella. Hylocomium* yields *Rhytidium, Rhytidiadelphus,* and *Rhytidiopsis.* Several other genera are split out by Fleischer, but not yet accepted by Grout. Even the much pared genus *Hypnum* still yields new genera, for example: *Brotherella, Heterophyllium, Ptilium,* and *Ctenidium. Plagiothecium* is subdivided into *Plagiothecium* (sensu stricto), *Taxiphyllum,* and *Isopterygium.* Grout considers these as subgenera, whereas Fleischer considers them as genera *in different families!* This very nicely illustrates the local viewpoint versus the cosmopolitan.

"I predict that I shall see all present subgenera become genera within my life-time. Splitting will continue almost anywhere in the mosses, perhaps most logically in the pleurocarpous groups. Hepaticae are in even more of a flux,

taxonomically. I am not unfavorably inclined or disposed toward these changes, for it is my conviction that most of the living forms are the tips of widely separated branches of the phylogenetic tree and are grouped together anyhow only because of man's passion for classification."

What I have just quoted from the above communication concerning the bryophytes is equally true of other forms. Let us, therefore, turn our attention to the flowering plants and for a little while consider the genus *Gaylussacia*, the huckleberries, with which many of us are familiar. The erection of the genera *Buxella*, *Decachaena*, and *Lasiococcus* to take care of our North American species of huckleberries has met with a great deal of opposition and I, too, have deplored the segregation.[2] But, fundamentally, it was sound, for the old classic genus is composed of four very definite groups of species: (1) The Buxifolieae (*Gaylussacia* H. B. K.), found mainly in the mountains of western South America, is composed of numerous species; (2) the Baccatae (*Decachaena* T. & G.), with its four species, is confined to eastern North America; (3) the Dumosae (*Lasiococcus* Small) ranges on the Coastal Plain from Newfoundland to Florida and Louisiana with two species, and occurs again with several additional in Brazil (a perfectly natural distribution); and (4) *Gaylussacia brachycera* (*Buxella* Small; this nomenclaturally a homonym) with an interesting distribution in small isolated areas from Tennessee to Pennsylvania and its morphological peculiarities, is plainly a relic out of the Early Tertiary and not closely related to the other huckleberries.

Had we been able to maintain the species with which we are most familiar in the genus *Gaylussacia* and erected new genera for those in South America, there would have been little protest. Apparently it is a common reaction among taxonomists—being human—that, so long as a genus is endemic in some remote part of the world it may be split as the student pleases, the splitting being hailed as a brilliant piece of research. But let one among us attempt, phyletically, to rearrange a genus with species in our own local areas—the rearrangement resulting in the necessity of learning new generic names—there is an immediate and loud protest. Even so, *Lasiococcus dumosus*, *Decachaena baccata* and *Buxella brachycera* are names with a strange and unfamiliar sound and I don't like them any more than you do. But, I have been asked, "Then why change them? We have known them as species of *Gaylussacia* for so many years." There is only one answer. If such an argument is to determine our criteria concerning the status of a generic name, then let us be purists and return these species to the genus *Vaccinium*, for they were known as *Vaccinium dumosum*, *Vaccinium resinosum*, and *Vaccinium brachycerum* for about a

[2] Bull. Torrey Club **62**: 129–132. 1935.

half-century prior to their inclusion in the genus *Gaylussacia*. The point is, none among us remember the clamor that arose when the botanists of another day had to learn to think of them as belonging to "that new-fangled genus *Gaylussacia*." From the standpoint of phylogeny, there is no more reasonableness in retaining these species in *Gaylussacia* than in returning them to *Vaccinium*.

Let us now turn our attention, briefly, to the Compositae. There immediately comes to mind the present controversy concerning the status of *Euthamia*. Is it to be a genus or merely a section of *Solidago?* If, however, we are truthful with ourselves, we must admit that the characters which we use to separate *Euthamia* from *Solidago* are of no less magnitude than those by which the basic species of *Solidago* and *Aster* are differentiated. Or conversely, if we return *Euthamia* to *Solidago* then, to be consistent, *Solidago* and *Aster* should be united. Or, for another example, the genus *Senecio*. Here is an open field for the taxonomist who wishes merely, either to describe a considerable number of new species or, as is not unknown to some of us, the pleasant experience of throwing a vast number of names into synonymy. Actually, however, the real opportunity for study in this genus lies in unraveling the various migration routes used, and the evolutionary mechanisms resorted to, by this cosmopolitan, highly divergent and exceedingly complex group of plants.

I am anticipating the question which the so-called conservatives will ask at this point. "Is it necessary that we have a whole host of new genera foisted upon us; will not the sub-genus satisfy your desire to express phyletic segregation?" The answer, flatly, is "No." Do these same "conservatives" advocate returning *Marchantia* to the Algae, all the species of lichens to *Lichen*, many of the mosses to *Bryum* and *Hypnum*, and a host of orchids to *Orchis?* So far, our science has been progressing steadily toward a rationalization between taxonomic categories and phyletic units, and I see no valid reason why we should make our nomenclatural system so rigid and unyielding that it would no longer serve to express what it traditionally has: *the rank and degree of relationship between organisms.*

This concern over "stability of names" has always been a point of discussion among botanists, and if taxonomic priority in the Spermatophytes goes back to the "Species Plantarum" so does the present controversy, for in 1753 Peter Collinson (probably the father of "modern" nomenclatural conservatism!) wrote to Linnaeus as follows:[3]

"I have had the pleasure of reading your 'Species Plantarum,' a very laborious and useful work, but my dear friend, we that admire you are much concerned that you should perplex the delightful science of botany with

[3] Clute, Willard N. The Common Names of Plants, p. 13. 1931.

changing names that have been quite well received and adding new names quite unknown to us. Thus, botany which was a pleasant study and attainable by most men, is now become by alterations and new names, the study of a man's lifetime, and none now but real professors can pretend to attain it. As I love you, I tell you our sentiments. . . . If you will forever be making new names and altering good and old ones for such hard names that contain no idea of the plant, it will be impossible to attain a perfect knowledge of botany."

Being thus fortified with the knowledge that today's controversies are not a new thing and buoyed by the hope that the science of taxonomy has not become stagnant, I trust that we may look upon our present minor tempests with the same patient humor with which we view those of the past. Thus, looking into the not-too-distant future, we may envision the day when our standard texts will list not more than a half dozen species of *Vaccinium* in the Americas for, after all, the high-bush blueberries of our eastern states are much more closely related to the secure and well-established *Thibaudia* of South America than to *Vaccinium Myrtillus*, the type of its genus, the one which Linnaeus described first because he knew it best.

Perhaps I speak with unreasoning rashness, but in a science where every thinking morphologist and vascular anatomist knows that the "Pteridophyta" are not a phylum; that the "family" Polypodiaceae is not monophyletic but, in the main, a miscellany of the end-products of the evolution of other basic fern families; and where nearly every taxonomist admits that the Compositae are polyphyletic and not a natural family—and yet does nothing about these things—it is small wonder that the honest phyletic revisionist, too often confused with the unreasoning splitter of genera, is looked upon as a botanical outcast and pariah.

I tell you, and I am serious, we as taxonomists must face the issue. Either we must take our place with those who are attacking the fundamental problems of biology, or we will degenerate into mere namers of specimens. We must either confine ourselves to the grinding out of a few lines of miserably inadequate Latin with *sp. nov.* and our names hooked onto it, or be biologists. The bifurcation is clear. And if we are to take our place in the body biologic, it can only be as phylogenists—students of evolution in the broad sense—with the naming of plants a mere incidental. In doing so, we will find it necessary from time to time to reconsider our premises for, with additional information, it will be necessary to reorganize our concepts and lay our course into new channels of thought.

At present, our nomenclatural system indicates phyletic relationship. If we continue this system—and I see no need to change it—the results of our work must then be reflected in the names we use. Actually, owing to

fortuitous segregation of the past, *the number of changes necessary would be much less than one might suppose.*

If I am correctly informed, the first organized part of botany was taxonomy. Morphology and comparative anatomy have long ago forgotten the manner in which they were born, and cytology has bred a line who look upon their sire with pity and a little contempt. It is perhaps advisable that they again be brought in as integral parts of the family circle. Yet, in honesty and fairness, their defection was no fault of their own. It was ours. When they were born we tolerated their blattings as we do those of infants. In adolescence we were blind to their needs and gave them little guidance and less help, refusing to see that as adults they might have something of their own and something to contribute to our needs. It is therefore little wonder that morphology, comparative anatomy and cytology, pursuing their own ways with but little concern and less guidance from their parent, should be little troubled with the trials and tribulations which now confront their sire.

Casting aside simile, I say: it is high time that we as taxonomists make better use of the findings, and particularly bring into play the techniques of the modern morphologist, the comparative anatomist and the cytologist. Frankly, those of us who blat loudest "Back to the fundamental truth—back to Linnaeus," are those who have made little or no use of the wealth of material already made available to us by the students in these other fields.

The space is limited and I cannot, here, present my case with specific examples where such studies have been made and the conclusions derived from them but, in general, if we were to apply the techniques available and reconsider the problems confronting us from the standpoint of phylesis, some of our existing genera would be combined and still others be broken down into their proper units. This, obviously, necessitates the change of some few names. But what of it? Should we, in deference to the non-taxonomists—a vociferous group who think of their branches of the science as being progressive—hesitate to modernize our science, even at the expense of a few changes of name? Do we as biologists hold that Aristotle taught only truth? In spite of their fad for "standardized plant names," do the horticulturists still use the nomenclature of Pliny? Do the physiologists feel the necessity of discussing their phenomena in the phraseology of Stephen Hales or Lavoisier? Do the ecologists use only the concepts of Warming? Do the anatomists describe their structures in the terminology of Marcello Malpigi or Nehemiah Grew? Do the cytologists consider Robert Brown the sole authority on nuclear phenomena? Are we, the taxonomists, then, to be stuck forever with concepts of the limits of genera as defined by Linnaeus, by Bentham, or even Asa Gray? If we are

honest with ourselves, we will admit that we have not felt any such necessity in the past. Nor do I see any present need of maintaining a stultitiously archaic *status quo* if, in holding to it, we impede the splendid progress already begun in a better understanding of fundamental plant relationships.

Perhaps we should adopt as our motto, not "Back to Linnaeus" but, "Forward to the truth." Perhaps, if we were not afraid of the puling croaking of certain of our confreres every time we broaden and particularize our concepts, we could put new life into old taxonomic bones, long interred in the musty vault of nomenclatural conservatism.

From an increasing number of laboratories there come rumblings of a rejuvenant taxonomy and I warn you, the workers in these institutions are not merely worms working in the corpse. When their further results come, as they recently have, there are those among us who may not like them, for a few plant families will be ripped apart and genera will be recast. Perhaps, with a regenerate and growing science—contributing more to botany than several additional lines to the latest supplement of the Index Kewensis when we revise a group; when we become a real part of biology —with emphasis on the true meaning of βιος—we then can move out of the top floors, the dusty attics and dim holes where they have pushed us and down where we belong—down on the first floor with the rest of those who, too, consider themselves botanists.

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The Cytology of Sporangium Development in Azolla filiculoides

Robert E. Duncan

(with 30 figures)

Introduction

The genus *Azolla* has long been of interest to investigators as one in which heterospory and a most striking case of tapetal behavior can be studied. In a classic monograph Strasburger (1873) presented the results of his morphological and histological researches on *Azolla*. He found that a leaf originates from the upper two ranks of epidermal cells of the stem. The first division of such a cell, in an anticlinal plane, forms an upper larger and a smaller lower cell. From these cells the two lobes of a mature vegetative leaf develop. In the development of a sporophyll the lower cell gives rise to a sporocarp and its hood-like covering instead of to the small lower lobe of a vegetative leaf.

Campbell (1893) considered that the hood represents a modified upper leaf lobe. Goebel (1898) held it to be merely an outgrowth from the under side of the upper leaf lobe. The sporocarp initial is foliar in origin (replacing the lower leaf lobe), grows for a time as does a leaf initial, then dichotomizes so that the ensuing sporocarps appear in pairs. Sud (1934) doubts the foliar origin of sporocarps in *A. pinnata*.

Strasburger (1873) reported that a sporocarp develops by means of an apical cell with three cutting faces, whose activity results in the formation of a columella or basal region from which sporangia later arise. About the base of the sporocarp initial appears a collar-like growth which, as the columella elongates, develops into the indusium or sporocarp wall, two cells in thickness. The primordia of macro- and microsporocarps are similar; a short-stalked macrosporangium is present in every case, but in a microsporocarp it ceases development early—being represented by the club-shaped end of the columella first described by Meyen (1836)—and microsporangia develop from initials at the base of the columella. In the developing macrosporocarp Campbell (1893) found that the apical cell of the columella forms a terminal macrosporangium. Goebel (1898) held the columella to represent an abortive macrosporangium.

In contrast to these points of view, Griffith (1844) observed that a terminal sporangium is present in every sporocarp but that in certain cases this sporangium collapses and other sporangia develop from below its base. Pfeiffer (1907) confirmed this observation, finding that the dif-

ferentiation of sporocarps is entirely dependent upon the persistence or non-persistence of a macrosporangium, which is always formed. "When a megasporangium has reached the stage in which eight spore mother cells are in synapsis some of the outer cells of the stalk enlarge and become apical cells of the young microsporangia." The eight macrospore mother cells give rise to thirty-two macrospores. If all but one disintegrate, the development of the microsporangia is suppressed. If, on the other hand, all the macrospores disintegrate, the microsporangia continue development, the macrosporangium collapsing and the sorus then becoming a microsporocarp. In each microsporangium appear sixteen spore mother cells whose division gives rise to sixty-four spores.

In the further development of a microsporangium, according to Strasburger (1889), a single tapetal layer is cut off from the central cell and sixteen microspore mother cells are formed by the division of the remaining central cell. The walls of the tapetal cells disintegrate and their protoplasts coalesce as the spore mother cells round up for meiosis. The tapetal plasmodium flows in among the spore mother cells; the contents of the microsporangium round up in the center, remaining connected only by thin cytoplasmic plates with the jacket of the capsule. The spore mother cells, apparently separate from one another, divide within this mass, in which the tapetal nuclei are uniformly distributed. The spores grow to their ultimate size and each becomes provided with an exine. The older spores are surrounded by clear areas which swell and coalesce so that finally a number of spores come to lie in a single vacuole; eventually, for each future massula, there is one such group of spores. The vacuole in which each group lies is surrounded and separated by plates of less vacuolate tapetal plasmodium; in consequence of vacuolar growth the sporangium attains its mature size. The plasmodial plates containing tapetal nuclei become thicker and more viscous; within the vacuoles granules derived from the plates appear and coagulate into delicate membranes. These massular membranes increase in thickness through the deposition of more granules; chemical tests show their composition to be similar to that of the walls of spores and pollen grains. The surrounding granular tapetum gives rise to glochidia, whereupon the remainder of this portion of the tapetum and the included leucoplasts disintegrate. The massulae are now mature.

Hannig (1911) found spindle-shaped nuclei in the tapetal plasmodium which he interpreted as representing stages in amitosis, since the number of nuclei increases. He, like Strasburger, considered the membranes of the massulae to be built up in vacuoles containing spores and nuclei by the coagulation of granules derived from the tapetal protoplasm surrounding the vacuoles. He noted that as the massulae mature the number of

tapetal nuclei diminishes; he gave also an account of the growth of the massulae. Glochidia develop from the exterior membranes of the massulae, while the latter are still lying in vacuoles, as irregular swellings which elongate and develop anchor-shaped heads. The walls of the glochidia become thicker at maturity. The pressure to which they are subjected in the sporangium keeps them prostrate on the surface of the massulae, but when the massulae are freed in water the glochidia spring upright in consequence of the shape of their basal portions. Campbell (1918) remarked that the apparent cellular structure of the massulae is probably the result of vacuole formation. He noticed that tapetal nuclei can be detected on the outside of the massulae almost up to the time of maturity.

Strasburger (1889) accounted for the development of the swimming organs and epispore of the macrospore in *A. filiculoides* in much the same way as for the formation of massulae. The three apically placed swimming organs are constructed of membranes built up in three vacuoles. The membranes of the chambered and warty epispore are similarly built up in small clear areas (vacuoles) oriented radially about the base and sides of the macrospore, which has now grown to fill the lower portion of the sporangial cavity. The whip-like appendages are formed, by the same method as glochidia, from the knobs of the epispore and from the apex of a stalk centrally located between the swimming organs. The chemical reactions of the membranes of the epispore and swimming organs are the same as those of the membranes of the massulae.

Hannig (1911) considered that the three apically placed vacuoles result from the fusion of smaller vacuoles in which the disintegrating macrospores lie, so that each of the three comes to contain approximately the same number of degenerating spores. Within these vacuoles the membranes of the mature swimming organs are built up; at maturity the functionless macrospores appear caught in the meshes of the swimming organs. The functional macrospore, too, lies in a vacuole within which the membranes of the epispore are constructed, so that the epispore plus the macrospore and the three swimming organs with their included functionless macrospores are respectively homologous with massulae. Hannig considered the whip-like appendages to be outgrowths of the surface of the vacuole in which the macrospore lies. Since the tapetal nuclei of both micro- and macrosporangium are passive and have no regular or fixed position, they play no part in the growth of the massulae. The periplasmodium, however, is a living protoplast which determines the location of the inclusions and constructs the epispore in either macro- or microsporangium.

Apparently the only statements in the literature regarding mitosis in *Azolla* are by de Litardière (1921). He observed 48 short chromosomes

in somatic divisions in *A. caroliniana*. In the telophases the chromatic material flows out from the ends of the chromosomes to form delicate fibers which anastomose with other similarly derived fibers. The chromosomes remain distinct throughout the interphases. In the prophases there is, first, a continuous spireme; then the anastomoses disappear and the chromosomes elongate somewhat, assume their characteristic short rod shape, and become double. The chromosomes then shorten; in the equatorial plate frequently appear linear series of chromosomes connected by fibers.

MATERIAL AND METHODS

In the present study plants of *Azolla filiculoides* Lam. bearing sporocarps collected at Palo Alto, California, and fixed by Dr. D. A. Johansen have been used. Fixations were made in formalin-acetic-alcohol, chrom-acetic, and Carnoy's alcohol-acetic fluid (five minutes) followed by chrom-acetic. Vegetative material of *A. caroliniana* Willd. and *A. filiculoides* Lam. growing in the botanical greenhouses of the University of Wisconsin was fixed in Randolph's, Belling's, and Karpechenko's modifications of Navashin's fluid, and in Carnoy's alcohol-acetic mixture. For the study of the cytoplasm Carnoy's fluid followed by chrom-acetic has been most successful; for nuclei, modifications of Navashin's fluid. Material fixed in formalin-acetic-alcohol was used only for morphological studies.

The material was dehydrated with alcohol or with dioxan. The use of the latter resulted in less hardening of the mature massulae than did that of the former. Chloroform or dioxan was used as an infiltrating agent and a commercial grade of paraffin as an imbedding agent.

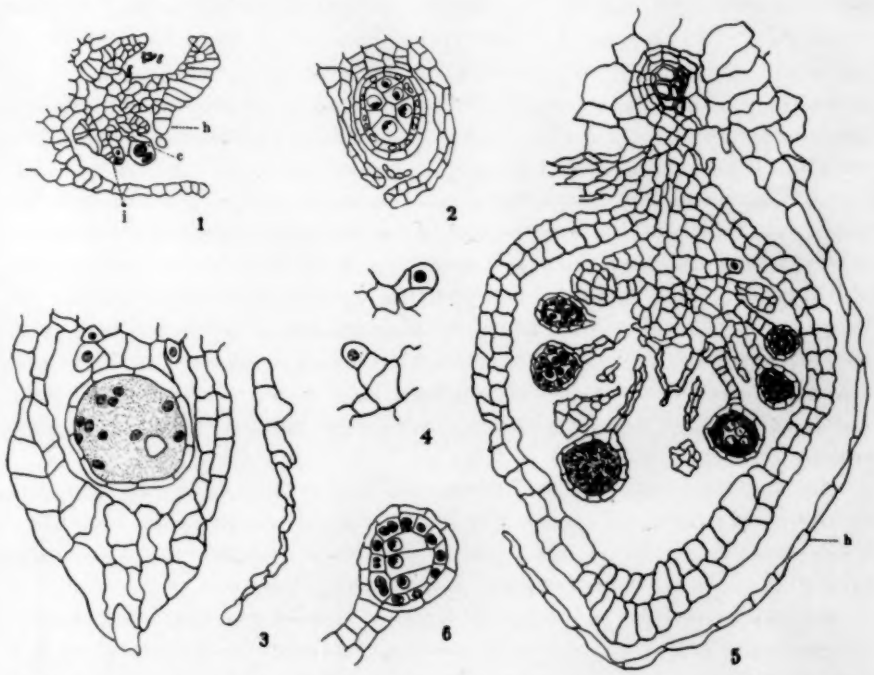
Sections were cut from 5 to 15 microns in thickness and stained with Flemming's triple stain or with Smith's modification of Newton's crystal violet-iodine. The latter was most helpful in determining the presence of nuclei at stages when their chromaticity is low, for the study of chromosome morphology and number, and for meiosis. By further modifying the crystal violet-iodine schedule, favorable staining of the tapetal cytoplasm was possible. For gross morphological study a safranin stain followed by a wash of dilute fast green was used.

OBSERVATIONS

Development of Sporocarps and Sporangia

In the material studied, sporocarps appear singly or more commonly in pairs; in no case were more than two observed together. The two of a pair may be of the same or of opposite "sexes." The sporocarp initial

takes the place of the lower leaf lobe; it has not been observed to dichotomize; it develops by means of an apical cell with three cutting faces, forming a columella. While the columella is still short a collar-like growth, the indusium or sporocarp wall appears about its base (*i*, fig. 1). By the time the apical cell has given rise to the columella (*c*) and a macrosporangium, these are surrounded but not closely invested by the indusium. The hood (*h*, fig. 5) arises from the lower side of the upper leaf lobe and grows out over the sporocarp.



All drawings were made with a camera lucida except those of the microspore mother cells.

Fig. 1. Longitudinal section of a sporophyll, the hood (*h*), and the sporocarp initial (*i*, indusium; *c*, columella). ×208.

Fig. 2. Longitudinal section of a young macrosporocarp showing an unelongated columella and a terminal macrosporangium. ×345.

Fig. 3. Longitudinal section of a macrosporocarp (not median of the distal portion of the sporocarp wall). The columella is elongated and microsporangial initials are developed. ×345.

Fig. 4. Longitudinal sections of initials arising from the epidermis of the elongated columella. ×345.

Fig. 5. Longitudinal section of a young microsporocarp showing a collapsed macrosporangium terminal to the columella and the basipetal sequence of microsporangia (*h* is the hood). ×315.

Fig. 6. Longitudinal section of a microsporangium. The microspore mother cells are entering synizesis while the tapetal cell nuclei are in the first wave of division. ×345.

Whether a macro- or a microsporocarp is ultimately to develop, a macrosporangium is always formed. The apical cell of the columella becomes the apical cell of the developing macrosporangium so that no more macrosporangia are ever formed (fig. 2). While meiosis is taking place in the macrosporangium the columella elongates and certain of its epidermal cells become the apical cells of microsporangial initials (figs. 3, 4). If, in the developing macrosporangium, one macrospore persists, the rudiments of microsporangia are suppressed; a macrosporocarp develops. If all the macrospores disintegrate, the macrosporangium collapses and the secondary initials below develop into microsporangia; a microsporocarp thus appears. The microsporangia arise in basipetal sequence from the columella, so that in a longitudinal section of a microsporocarp sporangia of various ages appear (fig. 5). As many as 130 microsporangia have been counted in a single sporocarp.

Sporangia of both types are leptosporangiate in origin and development. The stalk of the macrosporangium is short, relatively thick, and difficult to distinguish from the columella (fig. 3). The jacket, one cell thick, is formed by periclinal cell divisions on the anterior and lateral cutting faces of the apical cell; the remaining central cell gives rise to a single tapetal layer by several more periclinal divisions. The centrally located archesporial cell now remaining undergoes a series of three divisions in as many planes which form eight macrospore mother cells. The mature macrosporangium is usually ovate.

Each secondary apical cell possesses three cutting faces. In case these cells become active, each gives rise by divisions in its posterior faces to a stalk of two cell rows. The cells of the stalk elongate until complete maturity of the microsporangium. Rather early the apical cell cuts off on its anterior and lateral faces jacket cells; similar periclinal divisions of the central cell give rise to a single layer of tapetum. The remaining central archesporial cell undergoes a series of cell divisions in several planes to form 16 microspore mother cells. The shape of the microsporangium at maturity is spherical.

The divisions of the cells of each successive generation leading from archesporial cell to spore mother cells (five cell generations in the microsporangium, four in the macrosporangium) are simultaneous. Nuclear and cell divisions in the tapetal and jacket cells keep pace with the increase in the circumference of the sporangium up to the time of spore mother cell-formation.

Microsporogenesis and Development of Massulae

During synizesis in the microspore mother cells the nucleus of each tapetal cell divides mitotically so that these cells become binucleate (fig. 6).

In many cases each daughter nucleus divides almost immediately. Nuclear division is not followed by division of the tapetal cells. At about the time of the onset of leptonema in the nuclei of the spore mother cells, the walls of the tapetal cells disappear; their nuclei are now in various stages of a second series of divisions—mostly in the prophases, a few in metaphases and anaphases. Neither the first nor the second series of divisions of tapetal nuclei is perfectly simultaneous; but by the time the spore mother nuclei are in pachynema the tapetal nuclear divisions are completed and the daughter nuclei lie free and greatly crowded in a plasmodium occupying the periphery of the sporangial cavity (fig. 7). The spore mother cells have rounded up by this time, and are aggregated into a roughly spherical group.

When the anaphases of the homoeotypic division have been reached, the spore mother cells lie somewhat apart from one another in the cytoplasm of the tapetal plasmodium which has now begun to invade the central region of the microsporangium (fig. 8). The division of spore mother cells into tetrads is simultaneous and by means of cell plates oriented on spindles between each pair of nuclei (fig. 29).

The microspores become separated from one another and grow to about three times their original diameter. Tapetal nuclei as well as cytoplasm are now present in the central region of the sporangium. The walls of the immature microspores are thin; their protoplasts, as the spores grow, become increasingly vacuolate; the nucleus of each spore is somewhat flattened and lies near one side.

As a spore matures, a smooth wall is deposited. Apparently the wall layers are secreted by the spore protoplast itself, since no coagulation of granules derived from the tapetal plasmodium has been observed. Ultimately the wall consists of an outer relatively thick layer, next a thin darker layer, and within this a third layer somewhat less thick than the first but optically similar. Triradiate ridges are visible on the apical face of each spore at maturity.

After the spores have reached approximately their mature size they pass to the peripheral region of the sporangial cavity. The majority of the tapetal nuclei now lies in the central region (fig. 9). Many of the latter nuclei become spindle-shaped with irregular blunt ends (fig. 10). It is not improbable that cytoplasmic streaming carries many of the nuclei inward and the spores outward, the latter being caught sooner or later in the developing massulae. If so, the spores do not necessarily lie in the peripheral regions as earlier descriptions imply. This seems to be the case, since many of the spores, before their location is finally fixed, are apparently carried back to the center again after migrating to the periphery.

Spores frequently but not invariably seem to lie in vacuoles. A certain amount of shrinkage is to be expected in fixing material like the contents of a sporangium the concentrations of whose component parts vary greatly. The criterion of the efficiency of a fixation has been mainly the plumpness of the tapetal nuclei and the absence of "halos" about the nucleoli. The tapetal cytoplasm at the time of initiation of the massulae is very susceptible to osmotic changes, and the thin, delicate platelets of the massulae are frequently torn and crumpled, although many of the nuclei are plump.

The spindle-shaped nuclei are not fixation artifacts since they occur in the same region of the tapetal plasmodium with typically ovoid nuclei which possess rather evenly dispersed chromatic reticula and intact membranes. The spindle-shaped nuclei are not amoeboid, since their membranes are irregular and fragmentary. In addition, their chromatic networks become irregularly aggregated and their chromaticity increases; it would seem that such nuclei are disintegrating. Upon complete dissolution of the nuclear membrane, the chromatic substance may for a short period retain its stainability. Occasionally clumps of chromatic granules are found, but their infrequent occurrence suggests that the chromatin is rather quickly resorbed. Compression of developing vacuoles at times gives these disintegrating nuclei odd shapes and may cause great elongation.

The disappearance of the tapetal nuclei is haphazard at first but ultimately highly discriminatory, for soon the only ones left are those in the peripheral layer of the tapetal plasmodium and in intersecting plates of less vacuolate cytoplasm extending across the sporangium (fig. 11 *A*, *B*). The nuclei in these two regions retain their normal ovoid shape and sparse reticula.

Explanation of Figures 7–11

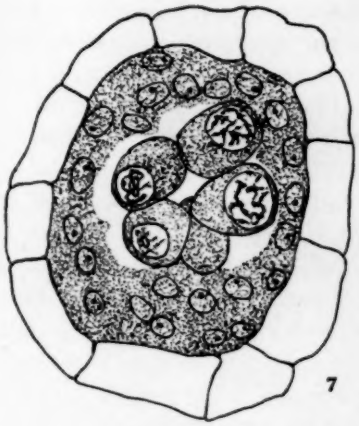
Fig. 7. Cross section of a macrosporangium. The microspore mother nuclei are emerging from synizesis and the tapetal walls have broken down, allowing the tapetal cell contents to coalesce and form a plasmodium. Another wave of tapetal nuclear divisions follows. ×750.

Fig. 8. Cross section of microsporangium. The microspore mother cells are separating from one another and the tapetal plasmodium is invading the central region of the sporangium. ×690.

Fig. 9. Cross section of a microsporangium. The microspores lie at the periphery while the tapetal plasmodium fills the sporangial cavity. Tapetal nuclei and vacuoles are irregulary distributed. ×690.

Fig. 10. Portion of the tapetal plasmodium. The homogeneous area is in the central region of the microsporangium. The spindle-shaped nucleus and the radially elongated vacuoles and fibers toward the outside are characteristic of the plasmodium in the regions where the massular rudiments develop. ×1975.

Fig. 11. A. Longitudinal section of a microsporangium. The massular rudiments containing spores and the intersecting nucleated plasmodial plates are shown. ×260. B. The platelets of a massular rudiment and an almost entirely disintegrated nucleus within it. × ca. 1000.



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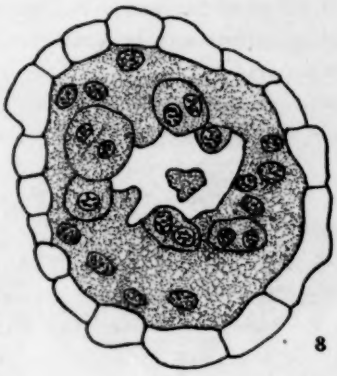

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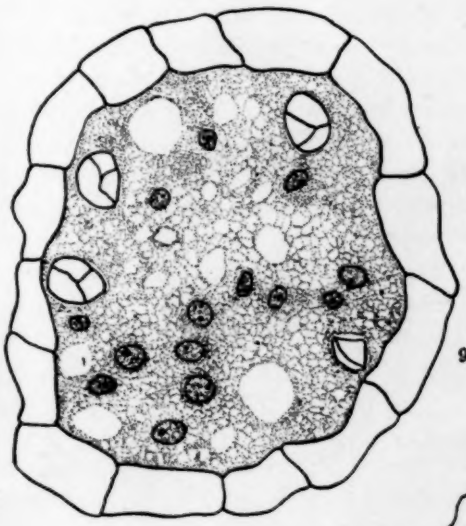

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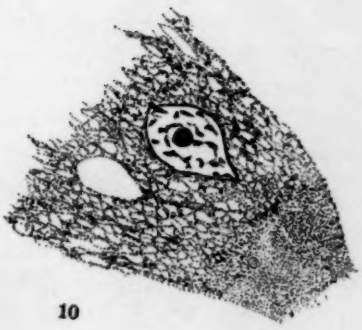

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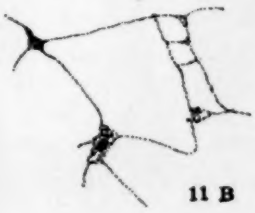


11 B

11 A

Before the disappearance of any of the nuclei the cytoplasm of the tapetal plasmodium is rather granular, the vacuoles present being small and indiscriminately scattered. While the nuclei are disintegrating, con-

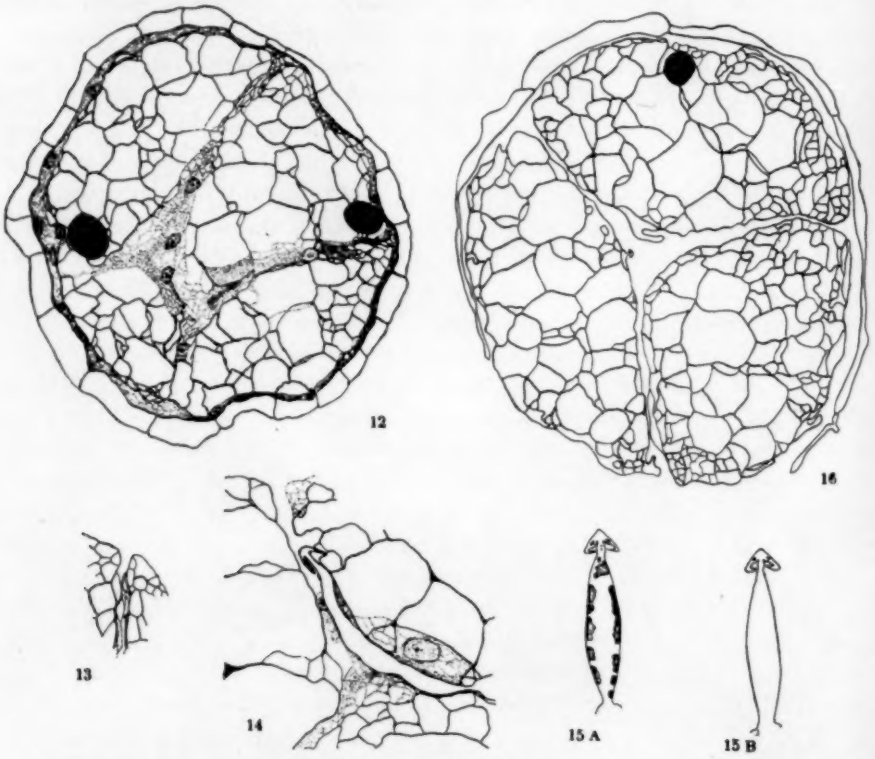


Fig. 12. Cross section of a microsporangium. The massulae are almost mature but are not yet separated. The plasmodial plates are just becoming vacuolate. × ca. 230.

Fig. 13. Portion of a plasmodial plate and massulae. The elongated vacuoles in the former will fuse and provide a means of separating the massulae. ×695.

Fig. 14. Glochidium forming on the inner surface of a massulae in a region where the tapetal plasmodium left is nucleated. ×860.

Fig. 15. Mature glochidia. A is the type described for certain plants; B is the common type. ×494.

Fig. 16. Cross section of a mature microsporangium. Three massulae are present. ×345.

siderable activity of the plasmodium is demonstrated by the arrangement of the granules into rows or into radiating catenate fibers (fig. 10). After the disintegration of the nuclei in the several regions (three to eight), between the intersecting plates in which the tapetal nuclei remain unaffected, the vacuoles of these regions increase greatly in size in consequence of some vacuolar fusion and of an actual increase of sap. The

maximum growth of the microsporangium occurs at this time; the capsule wall becomes greatly distended as vacuolar growth rapidly proceeds.

The from three to eight enucleate and vacuolate regions are rudiments of massulae (fig. 11 *A*). Each includes a variable number of microspores. The staining reaction of the intervacuolar material is slightly changed; it is compressed by the pressure of vacuolar growth into thin platelets in which may be found the remains of disintegrating nuclei (fig. 11 *B*). The delicacy of the platelets is demonstrated by the difficulty encountered in obtaining adequate fixation of the sporangium at this time. Later the platelets become more tenuous and hardened, a condition shown both by plasmolytic methods and by staining reactions; thereafter the vacuoles increase no more in size.

While construction of massulae is proceeding, the nuclei in the cytoplasmic plates separating the massular rudiments are still apparently healthy although they show some loss of chromaticity (fig. 12). When the membranes of the massulae assume their final texture, the nuclei of the plasmodial plates begin to disintegrate; the subsequent vacuolation is somewhat slower and more irregular (fig. 12). The vacuoles enlarging in these intermassular plates are flattened, probably in consequence of compression. The vacuolation of these plates may take place either almost immediately upon maturation of the included massulae or in the course of a relatively long period thereafter—depending upon the persistence or non-persistence of the nuclei. The elongated and flattened vacuoles in the plates fuse and the massulae become separated by a process resembling progressive cleavage (fig. 13). The cleaving process at times leaves a bit of cytoplasm with, usually, an included nucleus lying between the massulae.

As yet there is a complete peripheral sheath of tapetal plasmodium containing intact nuclei. This material and that left between the massulae by the cleaving process is the last active in the sporangium and is responsible for the formation of glochidia. Some of the peripheral layer may flow into the spaces left between the massulae or may remain, for a considerable part, in its original position. Early stages in the formation of glochidia have not been seen; by the time the massulae are separated the glochidia have formed. There is evidence that a nucleus is present at the base of each young glochidium and that the nucleus does not disappear until the glochidium is almost completely formed; there is evidence also that the glochidium is the result of a vacuolation and a constructive deposition of granules derived from the active portion of the plasmodium (fig. 14). Strasburger (1889) and Hannig (1911) described the walls of the glochidia as being of uniform thickness. In this study certain plants have been found all of whose glochidial stalks have walls made up of alternate thick and thin bands on the inner face (fig. 15 *A*); in other plants the

glochidia are of the uniformly thickened type (fig. 15 *B*). Once the glochidia are formed, the massulae are mature (fig. 16). Probably all the peripheral layer of tapetal plasmodium and any undifferentiated cytoplasm which may have remained between the massulae are exhausted in glochidium formation.

Development of the Macrospore and Accessory Structures

In the macrosporangium the sequence of tapetal nuclear divisions is similar to that in the microsporangium. The eight spore mother cells, all of which divide, and later the spores, are separated from one another by the influx of the tapetal plasmodium as in the microsporangium. The single macrospore which persists occupies a basal position in the sporangium; its apical faces are usually turned toward the apex of the sporangium (fig. 17). The macrospores above, although they deposit cell wall material, never grow materially and eventually become rather granular. They do not completely disintegrate, for traces of them may be found at the maturity of the epispore in the meshes of the swimming organs (fig. 20).

The persistent macrospore grows to occupy most of the lower part of the sporangium. The wall of this macrospore is constructed in a similar fashion to that of the microspores, but is thicker and is traversed by canaliculi of varying diameter (fig. 18). Through these channels there may well be protoplasmic connections between the spore protoplast and the tapetal plasmodium, since plates of less vacuolate cytoplasm lie opposite their openings. In the apical region of the sporangium the disintegrating macrospores are scattered irregularly. These, in consequence of plasmodial activity, sooner or later come to lie in three groups (frequently one group opposite each of the three apical faces of the persistent macrospore).

In the region of each of these upper groups of macrospores the tapetal nuclei disintegrate and the plasmodial cytoplasm becomes increasingly vac-

Explanation of Figures 17–22.

Fig. 17. Semidiagrammatic drawing of a longitudinal section of a macrosporangium at the time of the initiation of the rudiments of swimming organs toward the distal end of the sporangium. Note the disintegrating macroscopores caught in the meshes of the rudiments and the basal functional macrospore. ×690.

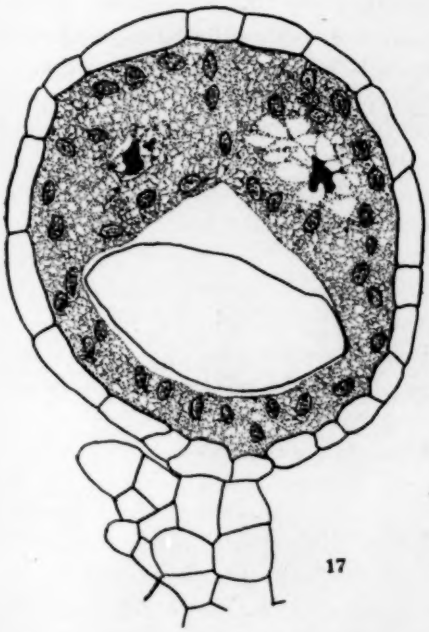
Fig. 18. Portion of the lower part of a macrosporangium from the macrospore wall outward. The vacuolated strips are rudiments of "warts." ×690.

Fig. 19. Portion of the epispore of the macrospore showing the whip-like appendages arising from the apex of a wart in an area where nucleated cytoplasm is present. ×1780.

Fig. 20. Longitudinal section of a mature macrospore and its appendages. This section does not show the attachment of the swimming organs to the columella. ×155.

Fig. 21. Polar view of a somatic equatorial plate. About forty chromosomes can be distinguished. × ca. 3800.

Fig. 22. Microspore mother nucleus in synizesis. × ca. 3800.



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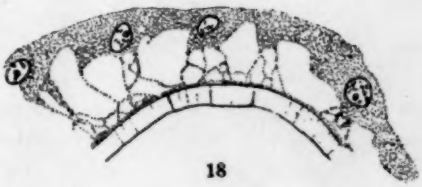

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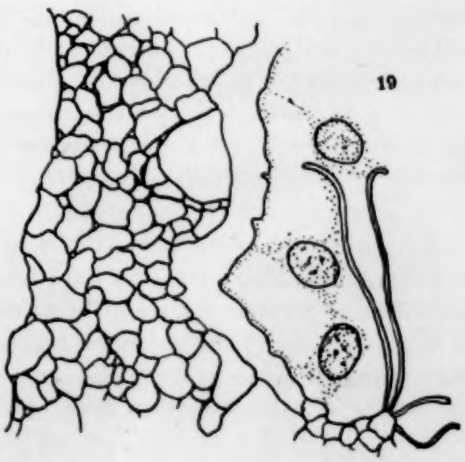

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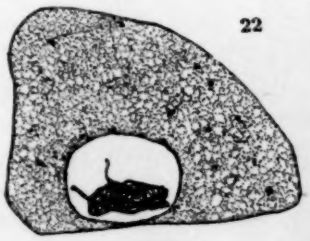

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uolate. These regions constitute the rudiments of the three swimming organs (fig. 17); they are homologous with the rudiments of massulae. The vacuoles in these regions grow, and the intervacuolar substance is flattened into thin platelets which are to harden and become parts of the mature swimming organ. In the region between each two adjacent rudiments, in a common central region, and in the peripheral region of the upper part of the sporangium, the tapetal nuclei are still intact and the plasmodium is active. The nuclei in these plasmodial plates between the rudiments, between each rudiment and the epispore formed on the macrospore below, and in the tapetum at the subapical periphery of the sporangium, next disappear. In each case the cytoplasm left becomes vacuolate and the intervacuolar substance is transformed into platelets. Those platelets arising at the periphery of the sporangial cavity are continuous with those of the initials of the swimming organs. As in the separation of the massulae, a process resembling progressive cleavage ensues in the areas between adjacent swimming-organ rudiments and between the initials and the epispore. In the cleavage zones, because of the compression of two developing rudiments or of a developing rudiment and the epispore, the vacuoles become flattened and fuse before the platelets become hardened. The common central region contains active cytoplasm and intact nuclei. This portion of the plasmodium gives rise at its apex to whip-like appendages (fig. 20). The remainder of the central region is transformed, by the disintegration of nuclei, a subsequent vacuolation, and the hardening of the intervacuolar substance, into the platelets of the mature structure of the columella, to which the swimming organs are attached. Here there is no fusion of vacuoles at a relatively late stage and no separation of the swimming organs at their inner faces from the columella or of the columella from the epispore of the macrospore, so that the three swimming organs are attached on their inner faces to the columella which, in turn, projects outward from the spore below.

The epispore is developed in a fashion comparable to the development of the massulae and swimming organs. The lower part of the sporangial cavity outside the space in which the macrospore lies is at first filled with tapetal plasmodium. In plasmodial plates radiating from the macrospore wall, generally extending from the canaliculi, and in a peripheral sheath of tapetal plasmodium which is intersected by these plates, the nuclei remain intact; in the areas bounded by the plasmodial plates, the macrospore wall, and the peripheral layer the nuclei disappear and vacuolation takes place. Upon vacuolation of the plasmodial plates after their nuclei have disappeared, the intervacuolar substance is transformed into the platelets of the chambered warts of the epispore (fig. 18). Apparently the remaining active peripheral portion of the plasmodium may be utilized in

several ways. In regions where the nuclei disappear relatively early, the intervacuolar substance is transformed into platelets—commonly at the apices of the warts of the part of the epispore already formed—or where the nuclei persist for a longer time, the plasmodium gives rise to the whip-like appendages at the apices of the warts (fig. 19) or forms of homogeneous layer in the depressions between them. The construction of the epispore is simultaneous with the formation of the swimming organs, each similar step being coincident in both areas. (Figure 20 illustrates the mature structure.)

Mitosis

Each nucleus of *Azolla* possesses one or two nucleoli, a sparse reticulum, and a large amount of karyolymph. The nuclei of the meristematic cells of root and stem tips and those of the cells of embryonic leaves never completely pass into a typical resting condition. This is true, also, of the nuclei in all regions in which there is rapid and repeated nuclear division, as in the tapetal cells and the sporogenous region. As the cells in root and stem tips and of the leaves approach maturity, and after the cessation of nuclear division in tapetal cells, the chromatic material of the nuclei becomes dispersed into a more or less uniform reticulum.

The interkinetic condition of the actively dividing nuclei is similar to that described by Rosenberg (1904) for certain cells of *Capsella*. Because of the close grouping of the chromosomes at late anaphases and early telophases the origin of the connecting fibers cannot be determined. After the chromosomes have separated somewhat, however, the greater part of the chromatic material forms aggregates equal in number to the chromosomes, connected with one another by fine threads. These aggregations are prochromosomes, or, according to Smith's (1934) interpretation, persistent points of spindle-fiber-attachment of the chromonemata.

In the early prophases the fine connecting threads disappear and the chromosomes elongate somewhat. The nucleolus persists until the chromosomes are fully formed. As the chromosomes pass to the equatorial plate they become greatly shortened. The chromosomes are not uniform in size, but in general they are short and rod-shaped (fig. 21). The equatorial plate is comparatively flat, there being no long chromosomes with trailing arms. In somatic plates the chromosomes have a tendency to be arranged in linear series by fine connecting fibers—evidently not all previous associating connections being lost until the time of the early anaphases. About forty chromosomes may be distinguished (fig. 21).

The separation of the daughter chromosomes is not strictly simultaneous. It is particularly noticeable that one or two pairs of daughter chromosomes migrate toward their respective poles much earlier than

the other pairs. Once their migration has begun, however, the precocious chromosomes lag and the remainder of the daughter chromosomes reach the poles at about the same time as the first to start. The chromosomes are so small that the point of spindle fiber-attachment is not easy to determine; no constrictions are recognizable.

Meiosis

The premeiotic divisions of the sporogenous cell nuclei seem to be similar to other mitoses. The spore mother cells are at first angular in outline; they do not round up until the nuclei are emerging from synizesis (fig. 22). The condition of the spore mother nuclei at the onset of meiosis does not seem notably different from the interkinetic condition of somatic nuclei. There is commonly a single nucleolus and a peripheral reticulum of chromatic material. The reticulum consists of numerous large, deeply staining bodies (the prochromosomes) connected, at least in part, by fine threads. In the early prophases the material on either side of the prochromosomes becomes increasingly chromatic; the time of disappearance of any of the connecting threads could not be determined. The leptotene chromosomes appear as elongated and at times moniliform threads, whose internal structure is indistinguishable. There is some tendency for pairing of certain parts of homologous chromosomes but this tendency does not seem to be carried to any great length. Such preliminary pairing is followed by a complete collapse of the threads into a contracted mass at one side of the nucleus. From this synizetic mass but few thread ends project (fig. 22).

In the cytoplasm of the spore mother nuclei appear irregular granules, which with the crystal-violet iodine technique stain like the chromatic material. These granules are scattered, some of them being close to the nuclear membrane. Since they persist throughout meiosis it seems probable

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Explanation of Figures 23–30

Fig. 23. Microspore mother nucleus in diakinesis. Note fibers connecting some of the pairs.

Fig. 24. Microspore mother nucleus in late diakinesis.

Fig. 25. Metaphase of heterotypic division in a microspore mother cell. Note the fibers attaching the two pairs of smaller chromosomes to two larger pairs. These smaller chromosomes commonly leave the equatorial plate before any of the others.

Fig. 26. Polar view of a heterotypic equatorial plate in a microspore mother cell. The chromosomes pairs cannot be counted with any certainty.

Fig. 27. Nuclei in a microspore mother cell at the completion of the heterotypic division. (Drawings at two different levels.)

Fig. 28. Homoeotypic division in a microspore mother cell. About eighteen chromosomes may be counted in one plate.

Fig. 29. Cytokinesis in a microspore mother cell.

Fig. 30. Tetrad of microspores.

All × ca. 3800.

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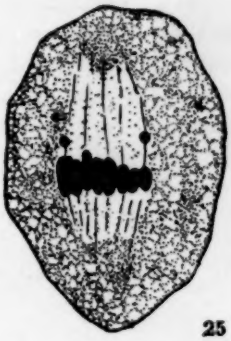

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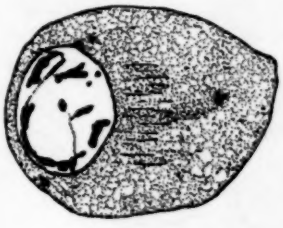

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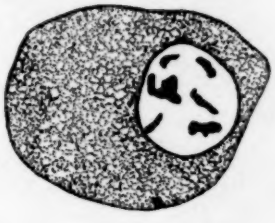

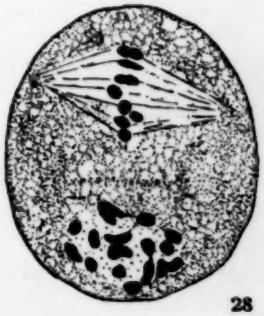

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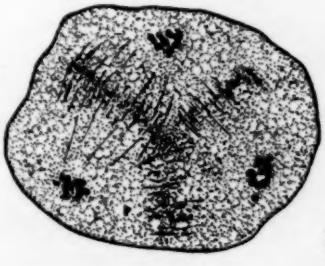

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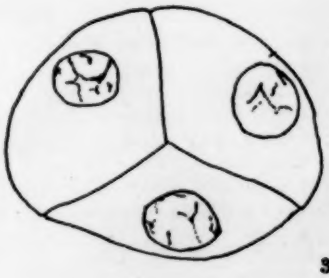

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that they may at times become involved in the spindle; occasionally they are found at the polar regions.

After emerging from synizesis the chromosomes pair so closely that whether or not each chromonema splits at this time cannot be determined. In fact the only evidences of pairing are the decidedly beaded appearance and the evident doubleness of a few free chromosome ends. During the period between diplonema and diakinesis the usual shortening and thickening of the chromosomes takes place. At diakinesis the chromosomes of a pair lie opposite each other, usually partly separated by a narrow clear zone. Each individual chromosome suggests by its moniliform appearance a double nature. The chromosome pairs lies in the peripheral region of the nucleus, occasionally connected with one another by slender fibers (fig. 23).

The chromosomes in the heterotypic equatorial plate are apparently thicker than at the time of diakinesis. Some of the fibers connecting the chromosomes are still evident. Two easily distinguishable pairs of spherical chromosomes are frequently attached to a pair of longer chromosomes so that each pair of longer chromosomes appears to bear a satellite (fig. 25). These same small pairs of chromosomes are the earliest to separate and leave the equatorial plate; the separation may even take place while the spindle fibers are becoming equalized in length. The chromosome pairs are in general closely grouped and occasionally several seem to form continuous chains (fig. 26); for these reasons the heterotypic plates are not satisfactory for determining chromosome numbers. The separation of the chromosomes of each pair is, however, regular. Daughter nuclei are reconstituted at the poles; there is little tendency to return to an interkinetic condition (fig. 27). The fibers of the first spindle form at the equatorial region a zone of granules which persists until the homoeotypic metaphase. The homoeotypical equatorial plate provides the most satisfactory place for determining the chromosome number (fig. 28). Counts made at this stage of the haploid number range from 18 to 20. The division of the spore mother cell is simultaneous by means of cell plates on spindles connecting each pair of nuclei (fig. 29).

DISCUSSION

The results obtained in this study indicate, as Strasburger (1873) found, that the sporocarp initial originates by dichotomy of the leaf initial and represents the transformed lower lobe of the leaf. The statement of Goebel (1898) that the sporocarp initial in turn dichotomizes is only indirectly confirmed by the observation of sporocarps in pairs and of their common place of attachment to the stem and their common vascular supply. The hood, as Goebel reported, is an outgrowth from the lower side of the leaf lobe. The sporocarp wall (indusium), in agreement with Strasburger's statement, originates as a collar of cells about the base of the initial.

The findings of Pfeiffer (1907) concerning the method of differentiation of sporocarps are confirmed in all respects. The development of the sporangia is leptosporangiate in type and basipetal in sequence.

The large number of nuclei in the tapetal plasmodium is accounted for by two waves of mitotic divisions: the first, relatively early before the tapetal cell walls break down and while the spore mother cells are rounding up for meiosis, when the tapetal cells become two- to four-nucleate; the second, after the tapetal plasmodium is formed while the nuclei of the spore mother cells are passing from leptonema to pachynema. No tapetal nuclear divisions have been found after the time of diakinesis in the spore mother cell nuclei. No stages in cell division following the first wave of mitoses and no incomplete nuclear divisions have been noted. No amitotic divisions were observed. The illustrations of Pfeiffer's (1907) paper show that she observed binucleate tapetal cells in both micro- and macrosporangia. Hannig's (1911) conclusion, that in *Azolla* the increase in number of tapetal nuclei is through amitosis after the tapetal cell walls have broken down and their protoplasts have united in a plasmodium, is incorrect. Kundt (1910) has found that the tapetal cells of *Salvinia natans*, also in consequence of a mitotic division, become binucleate. The conditions in *Azolla* as to the occurrence and the time of mitotic divisions in tapetal cells are closely in harmony with those described by Cooper (1932, 1933) and Smith (1933), who found that the nuclei of the tapetal layer in the microsporangia of various angiosperms divide mitotically while the microspore mother cells are in synizesis. Cooper (1933) noted that the tapetal cells become two- or, in case of a second mitosis, four-nucleate. Steil (1935) likewise has found nuclear divisions and occasionally incomplete cell divisions in the tapetum of the sporangia of *Ophioglossum* and *Botrychium*.

The results of the present study suggest that the formation of massulae, as well as of the swimming organs and epispore of the macrospore, involves a disintegration of plasmodial nuclei, a subsequent decadence of the plasmodial cytoplasm as indicated by vacuolation, and a direct transformation of the intervacuolar substance into membranes. It seems probable that the massular rudiments are areas wherein metabolic processes such as digestion and water intake are proceeding rapidly. The former process is suggested by the decrease in the amount of granular material in the cytoplasm of the tapetal plasmodium and by the disappearance of the chromatic clumps left by nuclear disintegration. In the strips of cytoplasm stretching across the areas interpreted by Hannig (1911) and Strasburger (1889) as vacuoles, chromatin clumps are still occasionally found. The ordering of the granules into radiating fibers and the increase in size of vacuoles suggest the entrance of water. Both this latter phenomenon and digestion cause much cytoplasmic streaming which in turn determines the location of the spores. The persistence of nuclei in certain areas

of the plasmodium slows down the decadence of the cytoplasm in the spheres of their influence, and any constructive process (such as formation of glochidia and of the whip-like appendages) takes place only in their presence.

Strasburger (1889) approached the problem of the construction of massulae and of the swimming organs and epispore of the macrospore as part of a general study of the growth of cell walls. His interpretation that the spores lie in clear areas, that these areas coalesce, and that the membranes of the various episporic structures are constructed in these areas indicates an attempt to homologize these various processes with the construction about the spores of a "perine."

Hannig (1911) attached more importance to the tapetal plasmodium than did Strasburger, who considered it only as a source of material for membranes. Hannig concluded that this plasmodium has the ability to order the location of its contents, but he too considered that the membranes of the massulae are built up in vacuoles in which granules and nuclei are floating. In this case the intervacuolar material also serves as a source of membrane material. He discounted the importance of the nuclei.

From the results of the present study it appears that the massulae are separated by a process similar to progressive cleavage. The same process partly frees the swimming organs from one another and from the epispore of the macrospore. Separation of the massulae comes about by the utilization of all the material of the plasmodial plates in building up the membranes of the massulae in the areas which the plates separated; consequently nothing lies between the massulae at their maturity.

A new type of structure of the glochidial stalk is described. It seems probable that this structure is not an intermediate stage in deposition of material on the stalk, but rather a variation from the more usual type.

The views herein advanced help to harmonize the massulae, the swimming organs, and the epispore of the macrospore with the homologous structures in *Salvinia*. Heinricher (1882) described the tapetum in that genus as giving rise to an amorphous mass in which the spores are imbedded. Kundt (1910) described the formation of the epispore in *S. natans* as taking place in essentially the same fashion, but in addition he observed that the tapetal nuclei disintegrate just before the vacuolation of the tapetal plasmodium. The condition in *Azolla* is more complicated only in that the tapetal plasmodium gives rise not to a single amorphous mass but to several which may be entirely separated as in the case of the massulae, or only partially so as in the case of the swimming organs and the epispore of the macrospore. Furthermore, the last active portion of the tapetal plasmodium forms the glochidia and the whip-like appendages.

The study of somatic chromosomes has led to results comparable to those of de Litardière (1921). The chromosomes, however, show more variety of shape and length than that author indicates.

Meiosis seems to be typical, although prochromosomes are present in the spore mother nuclei and fibers connect the chromosomes during diakinesis and in the equatorial plates of both heterotypic and homoeotypic divisions. The formation and persistence of such fibers may perhaps be evidence of partial end-to-end (spireme) arrangement of chromosomes in the prophases. The haploid chromosome set is about 20.

SUMMARY

The sporocarp initial replaces the lower lobe of a leaf; the hood is an outgrowth from the upper leaf lobe over the sporocarp. The "sex" of the sporocarp depends on the persistence or non-persistence of a terminal first-formed macrosporangium.

Two waves of mitotic divisions account for the increase in number of tapetal nuclei: first, the tapetal cells become two- or four-nucleate during synizesis in the spore mother cell nuclei; second, after the tapetal protoplasts have coalesced into a plasmodium and before the spore mother cells are in diakinesis, the free-floating tapetal nuclei divide again.

Massular rudiments are centers of cytolysis, related to nuclear disintegration and containing varying numbers of microspores. The intervacuolar material is transformed into the platelets of the massulae. Nucleated strips separating the rudiments meet a like fate. Vacuoles formed therein fuse, providing for the separation of the massulae. Glochidia are formed from nucleated cytoplasm on the massular surfaces.

Swimming-organ rudiments, containing disintegrating macrospores are cytolytic centers off each apical face of the functional macrospore. Separation of these organs from the columella is not realized. Membranes of the warts of the epispore of the macrospore are constructed by vacuolation of radiating strands of cytoplasm. Peripheral nucleated cytoplasm passes into a homogeneous layer in the depressions of the epispore or into whip-like appendages.

In somatic divisions about forty short straight or curved chromosomes appear. Prochromosomes are present in the nuclei of actively growing regions. Strands connecting chromosomes at diakinesis frequently persist until metaphase. Meiosis is typical; from eighteen to twenty pairs of chromosomes can be distinguished. Cytokinesis of the spore mother cells is by cell plates formed on spindles between pairs of nuclei.

This work was done at the University of Wisconsin under the supervision of Dr. C. E. Allen, whom the author wishes to thank for his helpful suggestions and interest.

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Notes on Alaskan Rust Fungi

J. P. Anderson

The writer has been interested in the Uredinales ever since he came to Alaska 25 years ago. During the earlier years specimens were sent to Dr. J. C. Arthur at Purdue University for determination, and reports of these were included in his work on the group in *North American Flora*, Vol. 7, and his *Manual of the Rusts of United States and Canada*. The latter work has been used by the author in determinations of recent collections and the following notes based thereon. In cases where the author was in doubt specimens were sent to Dr. George B. Cummins of Purdue University, Lafayette, Ind., for determination.

SPECIES NEW TO NORTH AMERICA

Puccinia Artemisiae-norvegicae Tranz. & Woron. Collected north of the Arctic Circle at Wiseman, August 1, 1939, on *Artemisia arctica* Less.

Puccinia Gymnandrae Tranz. This species was collected on *Lagotis glauca* Gaertn. on Nunivak Island, July 15, 1938.

SPECIES NOT BEFORE REPORTED FROM ALASKA

Uredinopsis Struthiopteridis Störmer, on *Athyrium cyclosorum* Rupr. at Ketchikan, August 4, 1927.

Chrysomyxa Cassandrae (Peck & Clint.) Tranz., on *Chamaedaphne calyculata* (L.) Moench. at Matanuska and Fairbanks in 1931.

Melampsora albertensis Arthur, on *Populus candicans* Michx. at Fairbanks in 1931 and at Wiseman in 1939 on *Populus tremuloides* Michx.

Phragmidium Andersoni Shear, on *Potentilla fruticosa* L. at Circle, July 19, 1935.

Phragmidium Rubi-idaei (DC.) Karst., on *Rubus subarcticus* (Greene) Rydb. (*Rubus strigosus* Michx. in part) at Curry, July 22, 1939.

Gymnoconia Peckiana (Howe) Trotter, on *Rubus arcticus* L. at St. Michael and at Stebbins, both near the mouth of the Yukon River, in 1938.

Puccinia arnicalis Peck was collected in 1939 at Healy and at Wiseman on two different but undetermined species of *Arnica*.

Puccinia conglomerata (Strauss) Schmidt & Kunze, on *Petasites frigidus* (L.) Fries, in the Talkeetna Mountains in 1931 and at Barrow and Wainwright on the Arctic coast in 1939.

PUCCINIA CRUCIFERARUM Rudolphi, on *Cardamine bellidifolia* L. in the Talkeetna Mountains, 1931.

PUCCINIA GIGANTEA Karst., on *Epilobium angustifolium* L. at Circle, July 19, 1939.

PUCCINIA GIGANTISPORA Bubak, on *Anemone globosa* Nutt. at Chitina, July 7, 1935.

PUCCINIA LIGUSTICI Ellis & Everhart, on *Conioselinum Gmelini* (Cham. & Schlecht.) Coult. & Rose on Gull Island in Lynn Canal in 1939, and on var. *kamtschaticum* (Rupr.) Hult. on St. Paul Island in Bering Sea in 1938.

PUCCINIA LINKII Klotz., on *Viburnum pauciflorum* Paylie at Skagway and Matanuska.

PUCCINIA MESOMAJALIS Berk. & Curt., on *Clintonia uniflora* (Schult.) Kunth, at Ketchikan and Hyder.

PUCCINIA OUDEMANSII Tranz., on *Parrya nudicaulis* (L.) Regel at Cape Lisburne, August, 1938. This is a new host, at least for America.

PUCCINIA OXYRIAE Fuckel, on *Oxyria digyna* (L.) Hill near Juneau in 1939.

PUCCINIA POLEMONII Dietel & Holway, on *Polemonium acutiflorum* Willd. at Gambell on St. Lawrence Island in 1938.

PUCCINIA POLYGONI-ALPINI Cruchet & Mayor, on *Aconogonum phytolaccaefolium* (Meissn.) Small (*Polygonum alpinum* Am. Auth.) at Golovin and Unalakleet in the northeastern Bering Sea region. It was abundant there in 1938.

PUCCINIA PULSATILLAE Kalchbr., on *Pulsatilla ludoviciana* (Nutt.) Heller at Healy in 1939.

PUCCINIA VAGANS var. EPILOBII-TETRAGONI DC., on *Epilobium anagallidifolium* Lam. in the Talkeetna Mountains in 1931.

UROMYCES FABAE (Pers.) de Bary, on *Lathyrus maritimus* (L.) Bigel. at Haines, Matanuska, and Unalakleet, thus extending from southeastern Alaska to the northern Bering Sea.

MELAMPSORA LINI (Pers.) Lév., on *Linum Lewisii* Pursh at Mile 240 on Richardson Highway. This is a little north of the Alaskan Range.

HOSTS NEW TO ALASKA AND EXTENSION OF RANGES

PUCCINIASTRUM PYROLAE (Pers.) Schroet., on *Pyrola minor* L. at Hyder in 1939. Previously reported from Alaska on *Pyrola asarifolia* Michx.

PUCCINIASTRUM SPARSUM (Wint.) Fisch. is reported from Alaska on *Arctostaphylos alpina* L. There is a red-fruited form of the host which has been described by Small as *Arctous erythrocarpa* which seems much more susceptible than the common black species. Collected at several localities in interior Alaska and as far north as Wiseman.

MELAMPSORELLA CERASTI (Pers.) Schroet. is common in the aecial stage on *Picea canadensis* (Mill.) B. S. P. throughout interior Alaska as far north as Wiseman.

MELAMPSORIDIUM BETULINUM (Pers.) Kleb., previously reported on *Betula kenaica* W. H. Evans from southeastern Alaska, was collected at Healy on *Betula glandulosa* Michx. and at Unalakleet on *Betula glandulifera* (Regel) Butler. The last may be a hybrid between *Betula alaskana* Sarg. and *B. glandulosa* Michx.

CHRYSOMYXA PYROLAE (DC.) Rostr. In addition to the hosts reported by Arthur from Alaska this species was collected on *Pyrola chlorantha* Sw. at Matanuska in 1931 and on *Pyrola minor* L. at Valdez in 1935.

MELAMPSORA BIGELOWII Thüm. The uredo and telial forms of this rust are very common on numerous species of *Salix* throughout the territory, but only once did I collect the aecial atage. This was in 1935 on *Larix laricina* (DuRoi) Koch at Mile 287 on the Richardson Highway north of the Tanana River.

MELAMPSORA ARCTICA Rostr. was collected on three additional hosts in 1938: *Salix arctica* Pall. at Point Hope; *Salix glauca* var. *glabrescens* Anders. at Deering; *Salix pulchra* Cham. at Cape Lisburne and at Nome.

TRANZSCHELIA SUFFUSCA (Holway) Arthur was collected at Healy, thus extending its range to central Alaska.

XENODOCHUS MINOR Arthur was collected on *Sanguisorba sitchensis* C. A. Mey. in the Talkeetna Mountains north of Matanuska. Previously reported from America only from Kodiak Island.

PUCCINIA ARENARIAE (Schum.) Wint. was collected on *Merckia physodes* Fisch. at Circle in 1935. This seems to be a new host for America.

PUCCINIA AREOLATA Dietel & Holway was collected on *Caltha asarifolia* DC. at Matanuska and on *Caltha leptosepala* DC. in the Talkeetna Mts. in 1931.

PUCCINIA CORONATA Corda was collected at Wiseman on ? *Calamagrostis canadensis* (Michx.) Beauv. in 1939.

PUCCINIA BISTORTAE (Strauss) DC. was collected at Wiseman on *Polygonum Bistorta* L. in 1939.

PUCCINIA FERGUSSONI Berk. & Br. was collected on *Viola Langsdorfii* Fisch. near Juneau in 1932.

PUCCINIA HEUCHERAE (Schw.) Dietel has been collected on the following additional hosts: *Mitella pentandra* Hook., *Tiarella unifoliata* Hook., and *Tolmiea Menziesii* T. & G. The range extends to the Alaska Peninsula.

PUCCINIA HIERACII (Schum.) Mart. was collected on *Hieracium albiflorum* Hook. at Hyder and on *Taraxacum mutilum* Greene at Fairbanks and at Wiseman.

PUCCINIA MILLEFOLII Fuckel was collected at Healy on *Artemisia elatior* (T. & G.) Rydb. This host is not given among hosts listed by Dr. Arthur.

PUCCINIA ORTONII Jacks. has been collected on *Dodecatheon frigidum* Cham. & Schlecht. in central Alaska, and on *Dodecatheon pauciflorum* (Durand) Greene and *Dodecatheon integrifolium* Michx. in southeastern Alaska. The last host is the same as that given by Arthur under the name *Dodecatheon Jeffreyi* Moore.

PUCCINIA POARUM Niels. The range of this species extends to the Bering Sea and Arctic. Collected on *Petasites frigidus* (L.) Fries on the Pribylof Islands and at Kotzebue.

PUCCINIA PORPHYROGENITA M. A. Curtis was collected on *Cornus suecica* L. at Juneau. This host is not given by Dr. Arthur.

PUCCINIA RETECTA Sydow occurs on the various varieties of *Anemone narcissiflora* L. as far west as Unalaska and to the north of Fairbanks.

PUCCINIA RUBIGO-VERA Wint. var. AGROPYRI (Erikss.) Arth. occurs on *Aconitum maximum* Pall. and on *Thalictrum kemense* E. Fries in the Aleutian Islands. Neither of these hosts is given by Arthur and they do not occur within the range of the rust as given in his manual.

UROMYCES HEDYSARI-OBSCURI (DC.) Car. & Picc. was collected on *Hedysarum Mackenzii* Richards at Wiseman and on an undetermined but different species of *Hedysarum* at Nome and Healy, thus adding two new Alaskan hosts and extending the range to north of the Arctic Circle to the Bering Sea.

UROMYCES PHACAE-FRIGIDAE (Wahl.) Hariot was collected at Eagle Summit on Steese Highway in 1935 and at Wiseman in 1939 on *Astragalus umbellatus* Bunge. This host is similar to if not identical with *Phaca frigida* L. Arthur reports this rust as occurring on *Phaca* sp. on Unga Island, southwestern Alaska; also in northern Europe.

UROMYCES POLYGONI (Pers.) Fuckel was collected at Seward and Palmer on *Polygonum aviculare* L. This extends the range westward.

AECIDIUM GRAEBNERIANUM P. Henn. was collected on a new host, *Limnorchis leptoceratatis* Rydb. This collection was made near Juneau.

SUMMARY

In this paper two species of rust fungi are reported as new to North America, 22 as not before reported from Alaska, 19 as occurring on 28 host species not previously reported as infected in the territory. In addition the known range of 13 species is extended.

JUNEAU, ALASKA

Notes on Plants of the Pacific Islands—II

F. R. Fosberg

The second paper of this series deals mainly with the Rubiaceae collected by Dr. Harold St. John in Fiji in 1937. The two regions visited, the wet central plateau of Viti Levu, and the Yasawa group of small islands, have not been explored previously by a botanist, so it seems worth while to record even the common species found there. Two new species are described in *Psychotria* and a new variety each in *Hedyotis*, *Ophiorrhiza*, and *Gynochthodes*. In addition to Rubiaceae, a new species is presented in *Phaleria* (Thymeleaceae) and two new combinations in *Diospyros* (Ebenaceae). The abbreviations (Ho), (Gr), and (NY) refer to the B. P. Bishop Museum, Honolulu, the Gray Herbarium, and the New York Botanical Garden, respectively, to which institutions I wish to express my thanks for the privilege of studying the material cited.

DIOSPYROS

Diospyros ferrea (Willd.) Bakh. var. nandarivatensis (Gill.) Fosberg. Caroline Is., Yap: Kanif, *Takamatsu 1966* (Ho); Takiol, *Takamatsu 1835* (Ho).

Diospyros ferrea (Willd.) Bakh. var. **palauensis** (Kanehira) Fosberg, comb. nov. *Maba palauensis* Kanehira, Bot. Mag. Tokyo **48**: 405. 1934.

Palau Is.: *Kanehira 499, 556, 406* (leaves narrow), *513* (all NY); Aimiriik, *Kanehira 2339* (NY) (cotype), *Nisida* (*Kanehira's?*) *2479* (NY) (isotype); Garasumao, *Takamatsu 1577, 1560* (Ho).

Differs from var. *littorea* in the slight rusty appressed pubescence on the young growth, and in the large, oblong-elliptic or somewhat obovate leaves with acutely contracted bases and heavy petioles. The leaves are up to 15 cm. long, 8 cm. wide, acuminate, coriaceous, glabrous or very early glabrate; fruit almost spherical, lightly appressed-pubescent, fruiting calyx somewhat cupulate, glabrate outside, tube sericeous inside.

Diospyros lateriflora (Hiern) Bakh. Fiji: Yasawa Group, Waya Island, Nagua, alt. 1300 ft., *St. John 18167* (Ho). Native name *bamba;* fruit edible.

Diospyros samoensis Gray, Proc. Am. Acad. **5**: 326. 1862. *Diospyros vitiensis* Gillespie, Bishop Mus. Bull. **74**: 14. 1930. Tonga Is.: Eua, Liku Terrace, *Parks 16321* (Ho).

Bakhuizen (Bull. Jard. Bot. Buit. III, **15**: 225–226. 1938) with some doubt reduces both *D. vitiensis* Gillespie and *D. longisepala* Gillespie to

synonymy with *D. samoensis* Gray. This seems correct for *D. vitensis*, but the narrow calyx lobes and flat calyx disk seem sufficient to separate *D. longisepala* as a variety.

Diospyros samoensis Gray var. **longisepala** (Gill.) Fosberg, comb. nov. *Diospyros longisepala* Gillespie, Bishop Mus. Bull. **74**: 14. 1930. Fiji: Yasawa Group. Waya Island, north of Yalobi, woods along Olo Creek, alt. 800 ft., *St. John 18121* (Ho) (differs from Gillespie's description in having slightly longer sepals, slightly shorter seeds, and broader leaves with a rounded base).

PHALERIA

Phaleria ixorioides Fosberg, sp. nov. Arbor parva glabra; folia oblonga vel ovato-oblonga apice acuminata basi cordata subsessilia, petiolo crasso 2–3 mm. longo, costa basi crassa; bracteae late cordatae 1 cm. latae 7 mm. longae, membranaceae; flores albi 5 cm. longi extus glabri intus sericeo-villosi, lobis 4, subpatentibus, 6 mm. longis; gynaecium glabrum 4 cm. longum, squamis obtusis.

Small tree 5 m. tall, trunk 3 cm. thick, vegetative parts glabrous, internodes terete, wrinkled when dry, elongate; leaves oblong or ovate-oblong, apex acuminate, base cordate, subsessile, chartaceous, petiole 2–3 mm. long, very thick, base of midrib also thickened, blade up to 18 cm. long, 7 cm. wide, usually 10–15 cm. long; bracts subtending flower head broadly cordate, obtuse, about 1 cm. wide, 7 mm. long, membranous; flowers white, fragrant, about 9 in a head, peduncle about 1 cm. long; perianth 5 cm. long, glabrous externally, silky-villous internally, tube gradually enlarged upward to 3 mm. wide, lobes 4, ovate, somewhat spreading, 6 mm. long; anthers 8, oblong, in two sets of 4 each, the upper inserted in throat, the lower about 4 mm. below throat; pistil glabrous, 4 cm. long, stigma 5 mm. long, enlarged, spindle-shaped, style filiform, ovary cylindrical, 1.5–2 mm. long, scales broad, obtuse; fruit not available.

Fiji: Yasawa Group, Waya Island, north of Yalobi, woods along Olo Creek, *St. John 18123* (Ho) (type).

Native name *tarutaru*, "used medicinally for scabies."

Related to *P. pulchra* Gillespie, resembling it in general appearance, but larger-leafed, with smaller bracts and white flowers 5 cm. long. Strikingly similar, in general appearance, to certain species of *Ixora*, hence the name.

BADUSA

Badusa corymbifera (Forst.) Gray. Fiji: Yasawa Group, Waya Island; Nagua, *St. John 18163, 18099* (Ho); Nakawa Gulch, w. side Batinareba, *St. John 18133* (Ho).

DOLICHOLOBIUM

Dolicholobium MacGregori Horne ex. Bak. Fiji: Viti Levu, Tholo East, Wainimala Valley, Wainamo Creek, Matawailevu, alt. 1600 ft., *St. John 18219* (Ho).

NEONAUCLEA

Neonauclea vitiensis Gillespie. Fiji: Viti Levu, Tholo East, Wainimala Valley, south of Matawailevu, alt. 800 ft., *St. John 18375* (Ho).

This species should be further investigated. The specimen cited above, though with only old shattered inflorescences, shows that the fruits were pedicellate, a fact not mentioned in Gillespie's description.

HEDYOTIS

Hedyotis auricularia L. var. **melanesica** Fosberg, var. nov. Caulis adpresso-pubescens glabratus; folia lanceolata acuminata breve petiola, 6–8 cm. longa, 1.5–2.5 cm. lata.

Stems appressed-pubescent, glabrate; leaves lanceolate or elliptic lanceolate, acuminate at apex, acute at base, 6–8 cm. long, 1.5–2.5 cm. wide, shortly petioled; stipules pectinately cut, hirtellous; inflorescences axillary, few flowered (3–10), not strongly congested but fusing to present the appearance of a whorl; corolla white; fruit 1.5–2 mm. long, calyx lobes erect, 1.5–2 mm. long in fruit, apex of fruit not strongly umbonate, fruit apparently indehiscent.

Fiji: Kandavu, hills above Namalata and Ngaloa Bays, alt. 200–400 m., *A. C. Smith 157* (NY) (type). Viti Levu, Tholo East, Wainimala Valley, Matawailevu, alt. 1600 ft., *St. John 18281* (Ho). Without loc., *U. S. Expl. Exp.* (NY). New Hebrides: Eromanga, Dillon Bay, alt. 400 m., *Kajewski 352* (NY).

Probably common in New Caledonia, though I have seen no specimens. Approached by certain Malaysian specimens, but on these the pubescence is more abundant and not so strongly appressed.

This variety is probably the plant Guillaumin (Not. Syst. **3**: 160–161. 1915) had in mind as *Oldenlandia crataegonum*, based on *Hedyotis crataegonum* Spreng. However, in the same publication he demonstrated that the latter was based on a Rumphian plant which Merrill (Int. Rumph. Herb. Amb. 479, 1917) shows to be *H. verticillata* (L.) Lam., a different species, and on a plant from Isle of France (Madagascar), which is a *Spermococe* or something of that affinity, having only one seed in a cell. Therefore the specific epithet *crataegonum* can have nothing to do with the Melanesian plant. This variety is close to two forms found in southeastern Asia and Malaysia, which, though having large leaves similar to those of var. *melanesica*, have, in one, spreading pubescence, and in the other greatly congested, multiflorous inflorescences.

According to St. John, a decoction of the leaves is used in Fiji as medicine for headache. Native names: *poroporo-i-langi* (Fiji), and *noo-lay-yelong* (Eromanga).

HEDYOTIS FOETIDA (Forst.) J. E. Smith in Rees Cyclop. 17, pt. 2, 1811. *Oldenlandia imberbis* Guillaumin, Not. Syst. 3: 161, 1915.

Examination of specimens from New Caledonia: without locality, *Franc 3074* (NY); Mts. of Gatope, *Vieillard 2711* (Gr), the former determined as *O. imberbis* by Guillaumin; shows that they are identical with the widespread *H. foetida*, extending the known range of that species to New Caledonia.

OPHIORRHIZA

OPHIORRHIZA LEPTANTHA Gray, Proc. Am. Acad. 4: 312. 1860. *Ophiorrhiza laxa* Gray, l. c.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18328* (Ho).

Gillespie (B. P. Bishop Mus. Bull. 74: 26–27. 1930) united these two species. This is probably correct, but the striking variability in such characters as shape of inflorescence, length of pedicels, number of flowers, etc., suggests that there may be subspecific entities present in the species. One of these that seems obvious, even in the absence of much material, is described below.

OPHIORRHIZA LEPTANTHA Gray var. **yasawana** Fosberg, var. nov. Folia membranacea, elliptica, 3.5–5 cm. longa, 1.5–2 cm. lata, integra ciliata; cyma gracilis, pauciflora, 3–4 cm. longa, 2–4 cm. lata; calycis lobi subulati.

Plant slender, about 4 dm. tall; leaves membranous, elliptic, 3.5–5 cm. long, 1.5–2 cm. wide, base acute or slightly attenuate, apex usually slightly acuminate, margin ciliate, strictly entire; inflorescence slender, few flowered, 3–4 cm. long, 2–4 cm. across, calyx lobes subulate, 1.5–2 mm. long; corolla lobes white, tube purple, corollas immature, probably to be rather smaller than in other forms of *O. leptantha*.

Fiji: Yasawa Group. Waya Island, woods along Olo Creek, north of Yalobi, alt. 800 ft., *St. John 18126* (Ho) (type).

Differs most conspicuously in the slender habit and small thin leaves with entire margins (rather than irregular as in most species of *Ophiorrhiza*, including *O. leptantha*).

Native name *karaua*.

MUSSAENDA

MUSSAENDA FRONDOSA L. Fiji: Yasawa Group, Waya Island, Yalobi, alt. 200 ft., *St. John 18008* (Ho).

CANTHIUM

CANTHIUM ODORATUM (Forst.) Seem. Fiji: Yasawa Group, Waya Island, Nagua, alt. 1200 ft., *St. John 18101* (Ho).

GYNOCHTHODES

GYNOCHTHODES OVALIFOLIA (Val.) Kanehira var. **Smithii** Fosberg, var. nov. Fructus magnus, compositus, 2–3 adnatus.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Matawailevu, alt. 2200 ft., *St. John 18298* (Ho) (type). Vanua Levu: Mbua, Lower Wainunu River Valley, alt. 0–200 m., *A. C. Smith 1716* (NY). Fulanga, 0–80 m., *A. C. Smith 1127* (NY).

Differs from the typical form from Micronesia (and Samoa) in the ordinarily much larger fruit, usually composed of two or three fused ovaries, though not invariably so. Single-ovaried fruits are not significantly different from those of plants from Micronesia and Samoa. The only compound ovary observed on material from outside Fiji was a single triple ovary on *Christophersen 2827* from Samoa, on which plant all the other ovaries are simple. In the compound ovaries, the individual ovaries are ordinarily arranged in a straight line, each contributing four cells (some usually abortive), forming two parallel rows. The fruit is oblong in transverse section.

Named for Dr. Albert C. Smith, of the New York Botanical Garden, botanical explorer of the Lau Islands and other parts of Fiji.

Native name *wa thoro;* "fiber used to tie home timbers together," according to St. John.

TIMONIUS

TIMONIUS AFFINIS Gray, Proc. Am. Acad. 4: 26. 1860. *Timonius sapotaefolius* Gray, l. c.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18339* (Ho).

These two plants seem to differ only very slightly, judging from the descriptions. A collection from Ovalau, vic. Levuka, *Gillespie 4468* (NY) may represent *T. sapotaefolius*. It is very similar to the rest of the material of this common species, except that the secondary veins are more or less obsolete. (My use of the term secondary veins corresponds to Gray's primary veins.) This seems to be the principal difference brought out by Gray. The closest relative of this species is apparently *T. Ledermannii* of Ponape, Caroline Islands.

MORINDA

The Fijian species of the *Morinda umbellata* relationship are not well understood, more material and especially field study being required. The identifications given here are to be considered tentative, with some explanation given with the two doubtful ones.

MORINDA BUCIDAEFOLIA Gray. Fiji: Viti Levu, Tholo East, Wainimala Valley, south of Matawailevu, alt. 1600 ft., *St. John 18241* (Ho).

Here taken to be the liana with elliptic to obovate, obtuse or rounded, reticulate leaves, with few secondary veins, fruits 1 cm. or less across, 4–7 at terminal node.

MORINDA FORSTERI Seem. Fiji, Yasawa Group, Waya Island: Nakawa Gulch, west side of Batinareba, alt. 600 ft., *St. John 18139* (Ho); north of Yalobi, woods along Olo Creek, alt. 800 ft., *St. John 18125* (Ho).

MORINDA MYRTIFOLIA Gray. Fiji: Viti Levu, Tholo East, Wainimala Valley, Matanatavo, head of Wainisavulevu Creek, alt. 3500 ft., *St. John 18309* (Ho).

Here taken to be the liana with small, elliptic, acute or slightly acuminate, chartaceous leaves, internodes 1–2 cm. long, heads few-flowered, 4–6 terminally, flowers white, bearded in throat.

ABRAMSIA

ABRAMSIA TRICHOTOMA Gillespie. Fiji: Viti Levu, Tholo East, Wainimala Valley, Raradawai to Nairairaikinasavu, Wainisavulevu Creek, alt. 2600 ft. *St. John 18225* (Ho).

IXORA

IXORA VITIENSIS Gray. Fiji, Yasawa Group, Waya Island: Nagua, alt. 1300 ft., *St. John 18154* (Ho) ("flowers white" but dried red), *18118* (Ho) ("fruit black, globose"); Naruarua Gulch, west side of Batinareba, *St. John 18047* (Ho) ("fruit black"); Nakawa Gulch, west side of Batinareba, alt. 800 ft., *St. John 18140* (Ho) ("flowers white, pink-tipped in bud; fruit black").

The variation in this species is perplexing, but more collections are necessary for a better understanding of it.

PSYCHOTRIA

PSYCHOTRIA CARNEA (Forst.) A. C. Smith. Fiji: Viti Levu, Tholo East, Wainimalu Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18340, 18327, 18318* (Ho).

Psychotria chrysophylla Fosberg, sp. nov. Arbor, ramulis glabris; folia oblonga, subcoriacea, glabra, petiolata; stipulae tenues, oblongae, 5 mm. longae, caducae, glabrae, non connatae; cyma terminalis, breve virido-brunneo-pubescens, pentachotoma; calyx infundibuliformis, 11–12 mm. longa, tubo extus pubescente, intus glabro, lobis extus vix pubescentibus; antherae 2.5 mm. longae, basifixae; stylus filiformis glabrus bifidus, corollae subaequalis.

Tree 7 m. tall, trunk 2 dm. through; branches terete, dark gray, glabrous, with short internodes; leaves oblong, blades up to 10 cm. long, 3.5 cm. wide, usually somewhat smaller, apex bluntly acute to very slightly acuminate, base obtuse or rounded to (rarely) acute or attenuate, subcoriaceous, glabrous, secondary veins widely divergent, prominent, 10–12 pairs, petiole 0.5–1 cm. long; stipules thin, oblong, acute or divided at apex, about 5 mm. long, caducous, glabrous, not connate or sheathing; inflorescence a single terminal long- pedunculate cyme, 5–7 cm. long, 4–6 cm. wide, shortly greenish- to brownish-pubescent, peduncle 3–3.5 cm. long at anthesis, pentachotomous, each branch trichotomous to pentachotomous, each branchlet bearing 2–3 subsessile or shortly pedicillate flowers; calyx funnel-form, 2.5 mm. long, with 4 short lobes, ciliate, soon reflexed or revolute, rounded or acutish, the whole pubescent outside; corolla tubular-funnelform, up to 11–12 mm. long, tube pubescent outside, glabrous inside, 8 mm. long, enlarged above, lobes 2.5 mm. long, 0.8 mm. wide, oblong, slightly pubescent outside, erect or ascending; anthers linear, 2.5 mm. long, basifixed, attached in throat; style filiform, glabrous, subequal with corolla, upper 1.2 mm. bifid into divergent, flattened lobes; fruit unknown.

Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18344* (Ho) (type). Grows in swampy rain-forests.

Native name *thauthau ni viti;* "decoction of leaves used as cough medicine."

Named from the yellow-green color of its leaves when dried, rather unusual in *Psychotria.*

Allied to *Psychotria vomensis* Gillespie but differing in the frequently uncut stipules, in the size, form, and pubescence of the inflorescence, the size and pubescence of the calyx, with its short reflexed lobes, and the externally pubescent corolla, with its oblong lobes.

Psychotria St.-Johnii Fosberg, sp. nov. Arbor, ramulis fistulosis tomentosis; folia chartacea acuminata valde albo-reticulata venulosa; stipulae calyptratae caducae valde rufo-tomentosae; cymae 3–4, graciles, laxae; calyx campanulata, albo-venulosa, 1 mm. longa, 2.5 mm. lata, vix lobata, glabra, in fructubus persistens; corolla hypocraterimorpha, alba, extus glabra, fauci barbata, lobis oblongis reflexis; antherae exsertae subbasifixae stylus glaber corollae

subaequalis supra incrassatus bifidus, frustus ovoideus irregularis, 6.5 mm.; longus, 3.5 mm. latus.

Tree 7–8 m. tall, branchlets fistulose, dark brown tomentose; leaves elliptic to oblong or slightly obovate, apex strongly acuminate, base acute to attenuate, blade as much as 23 cm. long, 9.5 cm. wide, usually much smaller, chartaceous, conspicuously white-reticulate venulose, main veins somewhat brownish pubescent beneath, especially when young, petioles variable in length, 1–4 cm.; stipules calyptrate, up to 3.5 cm. long, densely rusty-tomentose, caducous; cymes borne terminally in 3's or 4's which soon become lateral by development of a bud at the same node, thinly pubescent, peduncle slender, 2.5–3 cm. long, loosely branching several times dichotomously to tetrachotomously, ending in flowers on slender pedicels; calyx campanulate, white-reticulate-venulose, about 1 mm. long, 2.5 mm. broad, very shortly and very obtusely lobed, glabrous, persistent in fruit; corolla salverform, white, tube 3–5.5 mm. long, glabrous outside, throat strongly bearded with coarse white hair, lobes 5, oblong to oblong-ovate, about 2.5–3.5 mm. long, becoming reflexed, glabrous; anthers oblong or narrowly so, about 1.3 mm. long, exserted on filaments 2 mm. long, attached near the base, but sacs somewhat prolonged below attachment, inserted in corolla throat; style glabrous, subequal with corolla tube, thickened somewhat upward, the top 1.5 mm. divided into subulate lobes, disk much raised, fleshy; fruit irregularly ovoid when dry and not quite mature, about 6.5 mm. long, 3.5 mm. broad, pyrenes more or less tricarinate with middle keel strongest, keels somewhat broken, crowned with persistent calyx.

Fiji, Viti Levu, Tholo East, Wainimala Valley: Raradawai to Nairairaikinasavu, Wainisavulevu Creek, alt. 2500 ft., *St. John 18284* (Ho) (type); Raradawai, Wainamo-Wainisavulevu divide, alt. 2500 ft., *St. John 18279* (Ho); same loc., alt. 2800 ft., *St. John 18275* (Ho). Growing in moist woods to rain-forests.

Native names: *lewalekaleka, kali, aroasawa.*

Allied to *Psychotria taviunensis* Gillespie, but more pubescent, leaves cuneate-contracted at base, not so strongly acuminate, flowers larger, calyx campanulate, white-venulose, inflorescences more slender, longer. The fruit looks like that of *Psychotria carnea* but smaller. The calyx evidently represents an intermediate step towards that of A. C. Smith's genus *Calycodendron.*

Psychotria serpens L. Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18343* (Ho).

Psychotria tephrosantha Gray. Fiji, Tholo East, Wainimala Valley: Raradawai, Wainamo-Wainisavulevu divide, alt. 2500 ft., *St. John 18280* (Ho); Raradawai to Nairairaikinasavu, Wainisavulevu Creek, alt. 2600 ft., *St. John 18306* (Ho).

The latter specimen is described as a vine 8 m. long, climbing over trees, while the former is described as a shrub 7 m. tall.

PSYCHOTRIA TURBINATA Gray. Fiji: Viti Levu, Tholo East, Wainimala Valley, Raradawai, Wainamo-Wainisavulevu divide, alt. 2800 ft., *St. John 18267* (Ho).

CALYCODENDRON

CALYCODENDRON MAGNIFICUM (Gill.) A. C. Smith. Fiji: Viti Levu, Tholo East, Wainimala Valley, Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18329* (Ho).

CALYCOSIA

CALYCOSIA PETIOLATA Gray. Fiji, Tholo East, Wainimala Valley: Taunaisali, Wainisavulevu-Nubulolo divide, central plateau between the Wainimala and Singatoka Rivers, alt. 3800 ft., *St. John 18326* (Ho); Wainamo Creek, Matawailevu, alt. 1600 ft., *St. John 18217* (Ho).

CORRECTION:—In my recent paper *Notes on Polynesian Grasses* (B. P. Bishop Mus. Occ. Pap. **15**: 37–48, 1939) on page 46 in the synonymy of *Digitaria stenotaphrodes* Greek letter ε should be substituted for ξ, thus disposing of *Syntherisma pelagica* var. ε F. Brown. This typographical error was kindly called to my attention by Dr. H. St. John.

ARLINGTON, VIRGINIA

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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